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A STUDY OF THE SPERMATOGENESIS OF TWENTY-TWO SPECIES OF THE MEMBRACIDÆ, JASSIDÆ, CERCOPIDÆ AND FULGORIDÆ

A DISSERTATION
PRESENTED TO THE
FACULTY OF BRYN MAWR COLLEGE
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

BY
ALICE M. BORING

REPRINTED FROM
THE JOURNAL OF EXPERIMENTAL ZOÖLOGY
VOLUME IV
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BALTIMORE, MD., U. S. A.
1907

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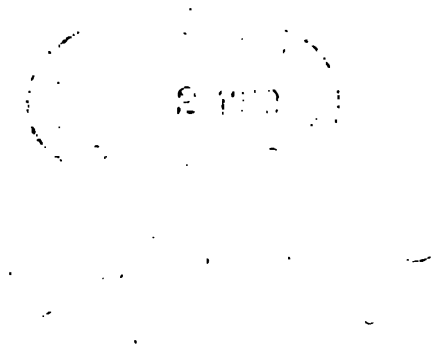

A STUDY OF THE SPERMATOGENESIS OF TWENTY-TWO SPECIES OF THE MEMBRACIDÆ, JASSIDÆ, CERCOPIDÆ AND FULGORIDÆ, WITH ESPECIAL REFERENCE TO THE BEHAVIOR OF THE ODD CHROMOSOME[1]

BY

ALICE M. BORING

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[1] A dissertation presented to the Faculty of Bryn Mawr College for the degree of Doctor of Philosophy.

INTRODUCTION

The purpose of this investigation is to extend, to some families of the Hemiptera Homoptera, the studies of McClung, Stevens, Wilson and others on the relation of the accessory or odd chromosome to sex determination. Except for the aphids, which have been extensively worked out by Stevens ('05a, '06a), Cicada tibicens (Wilcox '95) and Aphrophora quadrangularis (Stevens '06b) are the only species of this group whose spermatogenesis has been previously described. This study covers eight species of the Membracidæ, six of the Jassidæ, four of the Cercopidæ and four of the Fulgoridæ.

My work was begun at the suggestion of Dr. N. M. Stevens at Woods Hole in the summer of 1905, continued under Prof. E. G. Conklin, at the University of Pennsylvania, in the year 1905–06, and completed under Dr. Stevens, at Bryn Mawr College, in the year 1906–07. To both Dr. Stevens and Professor Conklin I wish to express my appreciation of their valuable suggestions and constant help and inspiration. I wish also to thank Dr. Herbert Osborn of Columbus, Ohio; Mr. E. P. Van Duzee, of Buffalo; Mr. H. C. Barber, of New York City, and Dr. H. Skinner, of Philadelphia, for the identification of material.

HISTORICAL REVIEW

Most of the work on the spermatogenesis of the tracheate arthropods has been done since 1890. Such studies as those of Bütschli ('71), La Valette St. George ('85), Platner ('86), Verson ('89), and Sabatier ('85) were concerned only with the formation of the spermatozoa, the arrangement of the cells of the testis into cysts, and the general mechanics of karyokinesis. The work of van Beneden ('84), Boveri ('87) and O. Hertwig ('90) on Ascaris, and Mark ('81) on Limax, turned the interest in the study of the sex cells to the chromosomes, while Weismann's daring hypothesis ('87) as to equational and reducing divisions added to the interest. By 1890, practically all investigations on spermatogenesis centered around the chromosomes in the spermatocyte divisions, and in

that year we find the first statement that one chromosome behaves differently from the others (Henking '90). Unfortunately there is the greatest confusion in the results for the next decade; but since Montgomery's suggestion ('01a) that synapsis means the conjugation of homologous maternal and paternal chromosomes, and its confirmation by Sutton's work on Brachystola ('00, 02, '03), there has been greater accord. As a consequence of this, certain fundamental theories are coming to rest on a firm foundation. The chromosomes are shown to keep their individuality from one cell generation to another. The real reduction in number is proved to be brought about by the joining of each paternal to a corresponding maternal chromosome in synapsis. It is found to make no difference whether the reducing or equational division comes first, but the distinction between these two divisions is constant, the one being the separating of the individual spermatogonial chromosomes, the other a simple splitting of these univalent chromosomes. In addition to this, recent work indicates that there is usually present throughout the Tracheata an odd chromosome in the spermatogonia, which behaves differently from the other chromosomes throughout its history. Still later work seems to establish the fact that this chromosome has no paternal mate, does not join any other chromosome in synapsis, divides in only one spermatocyte division, and enters only half of the spermatozoa. In some forms, a small chromosome is present as the paternal mate of this odd chromosome, but dimorphism of the spermatozoa results in either case.

The following review takes up the different observations on the Tracheata since 1890, and attempts to show how each helps to establish, or differs from, the above mentioned theories.

Arachnida

Wallace ('05) finds an even number of spermatogonial chromosomes, 40, two of these being larger than the others and different in behavior. They are condensed in the spermatogonial rest stage, and take an eccentric position in the equatorial plate. They remain separate from each other in the spermatocyte growth

period and do not divide in either spermatocyte division, as the other 19 chromosomes do, thus appearing in only one quarter of the spermatozoa. Wallace concludes that all the spermatozoa degenerate except those with the two odd chromosomes.

Montgomery in Lycosa ('05) finds an even number of chromosomes in the spermatogonia. Two of these he calls heterochromosomes, although the only characteristic that justifies this name is that they remain condensed in the growth period. They conjugate like the other chromosomes and divide in both divisions, all of the spermatozoa receiving one-fourth of the heterochromosome tetrad.

The results of neither of these investigators agree with the more recent work on the odd chromosome in spiders and other forms. If, as Wallace states, no spermatozoa develop except those containing the two odd chromosomes and the nineteen ordinary chromosomes, the eggs must all contain only 19 chromosomes, as the spermatogonial number is 40. Suppose each egg to have 19 chromosomes; fertilization by a spermatozoön with 19 + 2 chromosomes would give all the offspring 38 + 2 (19 + 2 in the reduced number), whether male or female; but according to Wallace's contention, the egg can have only 19; therefore it is impossible that all the spermatozoa, except those with the two odd chromosomes, degenerate. According to Montgomery, the heterochromosome in the spermatocyte is bivalent and divides in both divisions. Berry's work ('06) brings the odd chromosome in the spider into line with the odd chromosomes in other forms; it is a single chromosome in the spermatogonia, and divides in only the second division of the spermatocytes, resulting in dimorphism of the spermatozoa.

Myriapoda

Blackman ('05a, '05b) finds in Scolopendra heros and S. subspinipes an uneven number of spermatogonial chromosomes. Synapsis takes place in the late anaphase of the last spermatogonial division, all of the chromosomes uniting in pairs except the odd one. The odd chromosome divides only in the second spermatocyte division. The peculiarity here is that the other chromosomes

seem to undergo their reducing division when the odd chromosome is dividing equationally, but this is only a further mark of the individuality of the chromosomes, and does not furnish any evidence against Montgomery's theory of synapsis. Medes ('05) finds a similar condition in Scutigera forceps.

Orthoptera

Neither vom Rath ('91, '92) nor Wilcox ('95) noticed an odd chromosome in Gryllotalpa or Caloptenus, although both mention a nucleolus in the spermatocyte growth period which may be the same structure. They both insist that there are two reducing divisions; that is, two divisions that separate whole chromosomes from each other. This is probably due to a confusion in the use of the word chromosome. If we use the terminology suggested by McClung ('00), univalent chromosome in the spermatogonium, bivalent chromosome in the spermatocyte, and chromatid for each unit of the tetrad, the discrepancies in the work of vom Rath and Wilcox are cleared up. Vom Rath finds 12 spermatogonial chromosomes. In the growth period, the spireme splits into six rods, each of which forms a tetrad, or divides into four "chromosomes," as he expresses it. As he calls each chromatid a chromosome, he considers that he has two divisions which separate chromosomes from chromosomes; and therefore must be reducing; while in terms of the original spermatogonial chromosomes, one division is reducing and one equational. Wilcox falls into the same difficulty; he finds 12 spermatogonial chromosomes, and then the spireme divides into 24 "chromosomes," which form 6 tetrads. He had, in reality, 24 chromatids, and only one reducing division.

McClung ('00, '02a) has described the odd chromosome in the Acrididæ and Locustidæ. He worked on a number of forms and obtained uniform results. In the Orthoptera, this chromosome can be traced back into the spermatogonial rest stages. It divides only in the first spermatocyte division, giving dimorphism of the spermatozoa. In 1901, McClung suggested the theory which has since that time received substantial corroboration, that the dimor-

phism of the spermatozoa corresponds to the dimorphism of sex. McClung considers that the longitudinal division always precedes the reducing division, and thinks that this is important on account of the failure of the second polar body to be extruded in parthenogenetic eggs; but the work in the other groups of insects shows that the reducing division probably comes first as often as the equational.

Sutton's careful work ('00, '02) on Brachystola magna offers convincing evidence for the individuality of the chromosomes. Each pair of spermatogonial chromosomes becomes enclosed in a separate compartment of the nucleus, while the odd chromosome is in a vesicle shut completely off from the others. He suggests the application of Montgomery's theory of the union of maternal and paternal chromosomes in synapsis to Mendelian inheritance.

The observations of de Sinéty ('01) on the odd chromosome in one of the Acrididæ and in several Phasmidæ are entirely in accord with those of McClung; this chromosome divides in only one spermatocyte division, producing dimorphic spermatozoa. In one of the phasms, he finds a chromosome complex similar to that described later by McClung ('05) for Hesperotettrix, where the odd chromosome attaches itself to one end of a tetrad, forming a hexad which divides along the transverse axis of the tetrad, thus sending the odd chromosome and two chromatids of the tetrad to one cell, and two to the other. Unfortunately de Sinéty interprets both of the spermatocyte divisions as longitudinal, but on this point he is in the minority among the workers on Orthoptera.

Baumgartner ('04), in Gryllus domesticus, finds the odd chromosome in a separate vesicle as Sutton did for Brachystola, but he finds it dividing in the second division instead of the first. Stevens ('05a) in Stenopelmatus and Blatella germanica, and Otte ('06), in Locusta viridissima, find that the odd chromosome divides in the second division instead of the first. Evidently there is no fixed rule as to where the odd chromosome shall divide.

Voinov ('03), Montgomery ('05) and Zweiger ('06) all hold a different view as to the valence of the orthopteran odd chromosome; but as each has studied only one species of the order, while

the work of McClung, de Sinéty, Sutton, Baumgartner and Stevens covers numerous species in several families, we have a right to question the views of these other three observers. All three hold that the heterochromosome which they describe is formed from two spermatogonial chromosomes and divides in both spermatocyte divisions.

Moore and Robinson ('05) claim that the odd chromosome in Periplaneta americana is only a plasmosome which dissolves before each division and is reconstructed after it.

Odonata

The paper of McGill ('04) on Anax junius seems to show the same confusion which Wilson has discovered in Paulmier's work on Anasa tristis. McGill finds an even number of chromosomes in the spermatogonia, two of them small. These she identifies with the chromatin nucleolus of the rest stage and the odd chromosome, which divides in the first division and not in the second. If it could be shown that there are only 27 chromosomes in the spermatogonial plate, and that the odd chromosome is one of the larger ones, this form would fall into line with other work.

Lepidoptera

The early investigators in this field, Platner ('86) and Verson ('94) paid no attention to the chromosomes. I have not been able to read Toyama's papers, but the references to them by McClung indicate that the work is not very satisfactory. Stevens ('06b) gives a few figures for two species. There are two condensed bodies throughout the growth period, which fuse in prophase like the *m*-chromosomes in Alydus (Wilson, '05c), and this body divides in both divisions like the equal "idiochromosomes" of Nezara.

Coleoptera

The only work on the Coleoptera which deals with the heterochromosomes is that of Stevens ('05b and '06b) and of Nowlin ('06). Some of the beetles have an odd chromosome and others have an unequal pair in which the large member of the pair is the

maternal homologue of the odd chromosome, and the small member is the paternal mate which is lacking with the odd chromosome. In the Coleoptera, the reducing division comes first, the equational second. In this order of insects there is substantial proof of McClung's sex determination theory, as the oögonial equatorial plates have been shown to have the large chromosome, while the spermatogonial plates have the small one, and there is the same difference between the somatic plates of the males and females. The theoretical bearing of these facts will be discussed later.

Hemiptera

The chromosomes in this group are so large and few in number that they have attracted many workers, but in spite of this fact, there have been greater discrepancies than in almost any other group. Henking ('90) in working on Pyrrhocoris apterus, was the first to notice that in one spermatocyte division, one chromosome does not divide, thus causing a dimorphism of spermatozoa. He counted 24 chromosomes in the spermatogonia, and thought that this odd chromosome had the same valence as the others. He observed a large darkly-staining nucleolus in the growth period, although he did not associate a chromatic nature with it, or connect it with the odd chromosome of the spermatocyte mitoses. He formulated no theory to account for the dimorphism of the spermatozoa.

Wilcox ('95) records that there are 12 spermatogonial chromosomes in Cicada tibicens, and 24 spheroidal bodies in the spermatocytes, instead of a reduced number, results similar to those on Caloptenus femur-rubrum.

In Anasa tristis, Paulmier ('99) describes two small spermatogonial chromosomes, which form first the chromatin nucleolus in the growth period, then a tetrad which divides in the first spermatocyte division, and not in the second. Because this chromosome is small and appears in only part of the spermatozoa, he regards it as degenerating chromatin. Wilson ('05c), working over the same field, finds that Paulmier has confused two bodies, inasmuch as the two small chromosomes form a tetrad and divide in

both divisions, while the odd chromosome, which divides only in the first division, is the chromatin nucleolus of the rest stage and one of the large chromosomes of the spermatogonia. He maintains that Paulmier made a mistake also in the spermatogonial number, which is always odd. Foot and Strobell ('07), by the use of smear preparations and photo-micrographs, have attempted to show that Wilson is in error in his observations on the spermatogenesis of Anasa. They find that the odd chromosome acts essentially like any other chromosome, is made up of two spermatogonial chromosomes and divides in both spermatocyte divisions, its only peculiarities being that it does not appear as a tetrad in prophase and occasionally divides later than the other chromosomes in metaphase. They attempt to show that the chromatin nucleolus of the rest stage is not a chromosome, but dissolves before metaphase like a plasmosome. Wilson ('07) has carefully gone over his preparations and still thinks that his former conclusions are correct. There is need of more work with smear preparations to test their reliability.

Gross ('04), in his work on Syromastes, apparently confuses the *m*-chromosomes with the odd chromosome much as Paulmier did. In Pyrrhocoris apterus ('06) he finds the odd chromosome bivalent but dividing in only one spermatocyte division.

Montgomery ('01a) calls the odd chromosomes of the Hemiptera "chromatin nucleoli" and considers that they may vary in number and valence. He explains them as chromosomes on the way to disappearance during progressive evolution. His results show many discrepancies which have since been explained by Wilson ('05b and '05c).

Wilson groups the Heteroptera into three classes, those with an unequal pair of heterochromosomes, those with an odd chromosome and *m*-chromosomes, those with an equal pair of heterochromosomes. In the first class, the chromosome number in the second spermatocyte is one less than in the first spermatocyte. This is due to the fact that the conjugation of the unequal pair does not take place until after the first spermatocyte division. This is the most direct evidence yet found for Montgomery's synapsis hypothesis, for the small chromosome can be proved to be paternal,

and the large one, maternal. In the second class, the odd chromosome is homologous with the large maternal element in the unequal pair. The *m*-chromosomes are a pair, whose synapsis is delayed until just before the first spermatocyte division. The third class includes forms where there is neither an unequal pair, nor an odd chromosome, and therefore no visible dimorphism of the spermatozoa, but the fact that the equal heterochromosomes do not conjugate until after the first spermatocyte division, relates this class to the first class, and suggests that there may be a masked dimorphism, the equal heterochromosomes representing different characters, possibly, as truly as the unequal heterochromosomes where there is a visible dimorphism. Wilson cites a great deal of evidence for the individuality of the chromosomes, finding the same size relations between pairs of spermatogonial chromosomes as there are between single chromosomes in the spermatocytes. He elaborates McClung's sex determination theory, brings forward much evidence for the dimorphism of the spermatozoa, and shows that there is a corresponding dimorphism in the somatic equatorial plates of the male and female of several species of the Hemiptera heteroptera.

MATERIAL AND METHODS

My material was collected at Woods Hole in the summer of 1905, at Cold Spring Harbor in the summer of 1906, and at Bryn Mawr in the fall of 1906. The insects were caught in the usual sweep net, and the testes dissected out as soon as possible. Each testis consists of a group of several follicles, each attached by a separate duct to the vas deferens. The testes from the larvæ just ready for metamorphosis, and from the adults soon after metamorphosis, in most cases give all stages from the spermatogonia to the mature spermatozoa.

Before putting up material of any species, Schneider's aceto-carmine proved to be a quick and efficient reagent for determining whether the testes contained all the important stages. This fixes and stains the material at the same time. The testis is put on a slide in a drop of the stain, and the cells separated by pressing down the coverglass. The preparation is made air-tight

with vaseline, and in a few minutes, the chromatin is stained a deep carmine. The entire spermatogenesis might be worked out in such preparations, the only disadvantage being that the achromatic structures are not well fixed, and the preparations are not permanent. Camera drawings made from the aceto-carmine material, compared with those from sections of material fixed in the usual reagents, show the chromosomes in the former much larger in size. (Compare Fig. 198 with Fig. 205, and 201 with 207.) This difference is largely due to shrinkage in the usual fixing fluids and alcohols. The relative sizes and positions of the structures are the same in both kinds of preparations.

If the material showed the right stages, it was put up in various fixing fluids: Gilson's mercuro-nitric, Flemming's strong chromo-aceto-osmic, Hermann's platino-aceto-osmic, and Carnoy's acetic alcohol with sublimate. The dissecting was usually done in the fixing fluid, but the small quantity of material that was dissected in physiological salt solution and immediately transferred to the fixing fluid, showed just as good fixation, as is shown by the clear outlines of all the cell structures. A few cases of poor fixation were apparently due to the long time the insects were kept in captivity, as was sometimes necessary when the material was collected several miles from the laboratory, and immediate dissection was impossible. Gilson's mercuro-nitric was the fixative used most frequently, because it gives excellent fixation of the chromatin and is a very convenient fluid to use, but nearly all material was also put in one or both of the osmic mixtures, as these give better fixation of the achromatic structures. The Gilson was used for two to six hours, the Flemming and Hermann for twelve to twenty-four hours, followed by the same length of time in running water. The Carnoy was used but little. It does not fix so well as the Gilson. Its real value is for material where an aqueous fixative cannot be used.

After fixation, the material was run through the alcohols, cleared in xylol, and embedded in paraffine with a melting point of 52° C. Most of the sections were cut 5 μ thick, a few $3\frac{1}{2}$ μ and $6\frac{2}{3}$ μ.

Many stains were tried. The three giving most satisfactory

results were Heidenhain's iron hæmatoxylin, either without a counterstain, or with a slight tinge of orange G, thionin without a counterstain, and Auerbach's combination of acid fuchsin and methyl green. With iron hæmatoxylin, the long method gave the best results. Preparations in this stain furnish the best outlines for camera drawings, but for work in spermatogenesis, there is the disadvantage that it often stains plasmosomes and chromosomes alike. Thionin has proved a valuable stain for distinguishing between chromatic material and plasmosomes. With this material the best results are gained by leaving the slides in the stain from one to five minutes, rinsing off with water, and differentiating under the microscope with 95 per cent alcohol. The basichromatin holds the stain as a navy blue or dark purple, depending upon the material; while the plasmosome and oxychromatin either take a very pale blue, or hold no color at all. The Auerbach stain also gives differentiation between basi and oxychromatin, the odd chromosome standing out bright green in the rest stage against the pink spireme or scattered oxychromatin.

OBSERVATIONS

Membracidæ

In the Membracidæ, the testes are situated ventrally, near the anterior end of the abdomen. They are white in color, and each follicle is round. Such ripe spermatozoa as are present are found near the duct and the spermatogonia are situated on the opposite side. The rest of the follicle is filled with the intermediate stages, grouped into cysts containing cells in about the same stage. The succession of these stages is rather difficult to follow in the Membracidæ, because the follicles are spherical and no one longitudinal section gives all of the stages. The only way to trace the development is to find cysts with most of the cells in one stage and a few in transition to the next stage. In this way, the links between the stages can be filled in. In the eight species from which my material was obtained, the general course of development is very similar, with only here and there a striking difference. I shall there-

fore describe in detail one species, Entilia sinuata, and then mention the chief points of interest in the other species.

Entilia sinuata

This form was found in September, at Woods Hole, on the leaves of the Golden Glow, and later near Philadelphia, on the wild sunflower.

The resting spermatogonia stain very lightly, as there are only a few basichromatin granules in the midst of much scattered oxychromatin (Fig. 1). When the cell is preparing for division, a heavy, rather darkly-staining spireme is formed with the chromatin aggregated at regular intervals along the linin (Fig. 2). A longitudinal split appears in this spireme, a slight indication of which can be seen in Fig. 2. The chromatin next becomes condensed and segmented, but these segments still retain their linin connections. The longitudinal split in each segment is also very conspicuous at this stage (Fig. 3). Condensation of the segments continues, there being first an elimination of the longitudinal split (Fig. 4), and then a shortening of the segments until they are about twice as long as broad, the form which they have as they enter the equatorial plate of the spindle (Fig. 5). They appear in the plate with their longitudinal axis at right angles to the longitudinal axis of the spindle and with the linin connections still intact. This division, therefore, is a longitudinal division, separating each chromosome into two parts along the line of the original longitudinal split, which appeared in prophase. A lateral view of the spindle in metakinesis also shows convincingly that this division is longitudinal (Fig. 6). The number of chromosomes in the spermatogonial division is 21 but it is impossible to pick out the odd chromosome. The chromosomes become so closely massed together in anaphase (Fig. 7) that one cannot tell whether the linin connections still remain intact, or the conjugation of chromosome pairs takes place here. By the time the cell division is completed, the new nuclear membrane has been formed, possibly as Conklin ('02) has suggested, by the joining together of the linin sheaths of the chromosomes after these have absorbed liquid from the cytoplasm (Fig. 8). A linin connection joining the chromo-

somes end to end is visible soon after they have lost their smooth contours (Fig. 9).

The last spermatogonial telophase is followed by a dense, darkly-staining contraction stage, which looks like a tightly wound spireme. Here the outlines of the chromosomes and their connections are entirely obliterated. The contracted mass occupies only a part of the nucleus, leaving a large clear space at one side (Fig. 10). This space appears in preparations where the fixation of other parts seems to be perfect, so it can hardly be looked upon as an artefact, as McClung ('00) at first claimed. I have used Wilson's ('05b) expression, "contraction stage" as simpler than McClung's "synizesis," for the most condensed period of "synapsis" as Moore used the term. The chromatin now goes through a series of changes comparable to those of Anasa tristis (Wilson '05c): (1) an early postsynapsis, with a fine spireme, much twisted on itself, still staining deeply, but filling the nucleus much more completely than in the contraction stage (Fig. 11); (2) a late postsynapsis, with the spireme filling the cell completely, less twisted, and staining unevenly (Fig. 12); (3) an early growth stage, with the spireme thicker, the basichromatin aggregated at regular intervals along the linin (Fig. 13); (4) a rest stage, where the spireme scarcely stains at all, and in the midst of the pale nucleus (in iron hæmatoxylin) there is one lens-shaped black body (Fig. 14), which, following Stevens, I shall call the odd chromosome. It is the "accessory of McClung, the "chromatin nucleolus" or heterochromosome" of Montgomery, the "chromosome spéciale" of de Sinéty, or the "heterotropic chromosome" of Wilson. From the action of similar bodies in related species, I am convinced that it must be present here in the postsynapsis and early growth stages, but the spireme stains so deeply and twists on itself so much that it hides the odd chromosome. In the succeeding stage, where the spireme becomes longitudinally split, the odd chromosome lengthens out and loses the smoothness of its outline, although not the intensity of its staining reaction (Fig. 15). The spireme next divides into ten segments, each retaining its longitudinal split (Fig. 16). Counting the odd chromosome, which remains closely applied to the nuclear membrane, there are now 11 chromatic

elements present in the nucleus. Just before the contraction stage, the spermatogonial chromosomes were joined end to end by linin connections, and out of the contraction stage there came a continuous spireme, which has passed through various stages and finally segmented. If the chromosomes conjugate end to end in the late anaphase (Fig. 8), as Fig. 9 might suggest, the longitudinal axis of the primary spermatocyte segments, or chromosomes, represents the longitudinal axis of the spermatogonial chromosomes. The presence of a massed anaphase and of the contraction stage makes it impossible to prove that this is the case here. It has, however, been proved for other forms (Sutton) and the agreement of all other steps in the process points to a possible similarity in this respect also. The 10 segments next become tetrads by the formation of transverse arms which always remain a little shorter than the longitudinal arms, and thus make it always possible to distinguish between the longitudinal and transverse axes (Figs. 17 to 19). While the tetrads and dumb-bells are forming, the odd chromosome rounds up again and becomes a lens-shaped body, still applied to the nuclear membrane (Fig. 20). It is in the dumb-bell form that the chromosomes usually enter the spindle (Fig. 24), but occasionally they are still in the form of cross-shaped tetrads (Fig. 22). This shows conclusively that the longitudinal axis of the dumb-bell is the same as the longitudinal axis of the tetrad, and that the first spermatocyte mitosis is a transverse division. That it is probably a reducing division can be shown by tracing back the development, and working out the corresponding axes: the division between the halves of the dumb-bell (Fig. 24) corresponds to a division along the lateral arms of the tetrad (Fig. 17), and that to a transverse section of the spireme segment (Fig. 16) and that to the separation of one spermatogonial chromosome from another, if we assume that each spireme segment equals two spermatogonial chromosomes joined end to end. This may be further evidence against McClung's ('00) contention that the reducing division is always the second. In the equatorial plate of the first spermatocytes the odd chromosome stands a little apart from the other 10 chromosomes, and is smaller in diameter (Fig. 21). It does not divide in the first spermatocyte division, but lags

behind the others in going toward the spindle pole (Figs. 25 and 27). The chromosomes mass together in the anaphase, so that as soon as the odd chromosome joins the others, it is no longer possible to distinguish it (Fig. 28).

The spindle fibers stand out very clearly, especially in the material fixed in Flemming or Hermann, and it is noticeable that the odd univalent chromosome is joined to only one pole by its mantle fibers, while the bivalent chromosomes are attached to both.

During the telophase the granules of a "Zwischenkörper" can be seen on some (Fig. 25) or all (Fig. 26) the spindle fibers. These show only in iron hæmatoxylin preparations which have not been extracted very thoroughly. In such preparations the centrosomes of the first spermatocyte division can also be seen (Fig. 23). They divide during the anaphase of the first division (Figs. 25 and 27) in readiness for the second division which succeeds the first without any reconstruction of the nucleus.

The chromosomes rearrange themselves (Fig. 29) into a plane at right angles to the plane of the first division, and soon form a regular equatorial plate. Half of the second spermatocytes contain 10 chromosomes (Fig. 31) and the other half 11 (Fig. 30), that is, 10 plus the odd chromosome. In the cells containing 11 chromosomes, the odd one does not differ enough in size to make it any longer distinguishable. In this division, all the chromosomes in all of the cells divide. The reasons for this conclusion are: (1) the lateral views of the metaphase (Fig. 32) never show one undivided chromosome among the other dividing ones, (2) all the chromosomes are attached by mantle fibers to both spindle poles, and (3) in the anaphase, there is never a lagging chromosome near one pole without a mate at the other pole (Fig. 33). That this division of chromosomes is at right angles to the first, that is, longitudinal and equational, is certainly conditioned by the formation of the spindle which is derived directly from that of the first division. The same fibers between the chromosomes and centrosomes remain intact, and as the centrosome divides, the chromosomes are pulled into an equatorial plate at right angles to the equatorial plate of the first spermatocyte division. This second division therefore corresponds to the preliminary longitudinal splitting of

the spireme in the growth period. One spermatocyte division is reducing and the other equational. In the anaphase, the chromosomes again become massed together (Fig. 34) and the nucleus is reconstructed by the formation of a nuclear membrane (Fig. 35). The "Zwischenkörper" is again noticeable in this telophase.

In the young spermatid (Fig. 36), the chromatin is still massed together and stains deeply. The spindle material remains as the "Nebenkern," as first described by v. La Valette St. George ('86) for insect spermatids. The chromatin soon scatters through the nucleus in definite clumps and it is evident that half of the spermatids contain a smooth round darkly-staining body (Fig. 37), while the other half do not (Fig. 38). Through several succeeding stages, this same fact is noticeable; *i. e.*, when the chromatin becomes more diffuse (Figs. 39 and 40), when it forms a pale network and the axial filament has grown out (Figs. 41 and 42), and even when the chromatin has begun to condense to form the head of the spermatozoön (Figs. 43 and 44). The method of determining whether this body is in only half the cells or in all is as follows: cysts of spermatids in various places were picked out and the number of cells with and without this body were counted in each cyst. In studying sections, it must be remembered that parts of some cells are in another section, so even if this body (x) were actually present in all the cells, it would not appear in all in any one section of a cyst. On the same principle, if it were actually in only half the cells, it would appear in less than half in any one section. In Entilia, this body appears in a few less than half of the spermatids. It always takes the chromatin stains, deep blue with thionin, and green with the Auerbach. As it resembles the odd chromosome of the first spermatocyte rest stages in staining reaction and contour, and as it appears in not more than one-half of the spermatids, a condition which the odd chromosome necessarily fulfills from the fact of its not dividing in the first spermatocyte division, we seem to be justified in concluding that the body x of the spermatids is a derivative of the odd chromosome of the spermatocyte. There is nothing unusual about the formation of the spermatozoön. The "Nebenkern" forms the sheath of the axial filament (Fig. 41), the acrosome differentiates from the cytoplasm at the apex of the

head, the head forms by condensation of the chromatin (Figs. 44 to 47), passing through one rather diffuse stage (Fig. 46).

Vanduzea arcuata

Vanduzea arcuata was found in abundance on the locust trees near Cold Spring Harbor in June. The spermatogonial plates show 17 chromosomes, varying in size (Fig. 48). It is not possible to arrange them all in pairs, but at least two large pairs are well marked (a_1 and a_2, b_1 and b_2). In the growth stage, the odd chromosome appears as a long, darkly-staining body, without a smooth contour. It is at first bent upon itself in different forms (Fig. 49), and later lies at full length along the nuclear membrane (Fig. 50), resembling the same stage in Entilia sinuata (Fig. 15). In the equatorial plate of the first spermatocyte division, there are 9 chromosomes, two of which are larger than the others (Fig. 51, *a* and *b*), corresponding to the four large ones in the spermatogonial plate; *a* is slightly larger than *b* just as a_1 and a_2 were slightly larger than b_1 and b_2. This point certainly counts as evidence that each spermatocyte chromosome represents not an indefinite segment of the spireme, but two individual spermatogonial chromosomes. The odd chromosome can be recognized by its eccentric position. Fig. 52 shows all the chromosomes but *x* in metakinesis, and in Fig. 53 *x* is passing to one pole undivided. Figs. 54 and 55 show variations in the position of *x* in anaphase; it does not always lag behind, but may even precede the other chromosomes to the pole. The second spermatocyte equatorial plates, containing 9 and 8 chromosomes, respectively, are shown in Figs. 56 and 57. Each has one large chromosome *a*, one not quite so large *b*, and six small ones of about the same size. Fig. 56 has a ninth chromosome of intermediate size which must be the odd chromosome, as *x* in the first spermatocyte plate has a corresponding intermediate size (Fig. 51). All the chromosomes divide in this division, including the odd one, as is shown in all of the lateral views of the metaphase (Fig. 58) and of the anaphase (Fig. 59). Half of the spermatids contain the odd chromosome, and half do not (Figs. 60 and 61).

Ceresa taurina

Three species of Ceresa were found near Cold Spring Harbor on the morning-glory vines and tall weeds, during the last three weeks of July. Unfortunately the chromosomes of the spermatogonial plates in all three forms are too close together to make it possible to count them. They all have the same reduced number of chromosomes and a peculiar deposition of chromatin on the nuclear membrane in the growth period. As this phenomenon is most pronounced in Ceresa taurina, I shall give the details for this form. In the contraction stage, the chromatin is massed at one side of the nucleus in a number of darkly-staining loops with their bases united in a dense flat chromatic plate, which stains more deeply than the loops (Fig. 62). As the loops spread through the nucleus, they stain less, making the contrast with the black plate more intense (Fig. 63). In the rest stage (Figs. 64 to 67), the reticulum does not take basic stains at all; the chromatin plate appears in various forms, sometimes continuous and sometimes broken up into two, three, or four parts. By the time a split spireme is formed, it has been almost entirely dissolved (Fig. 68), and in the prophases, no trace of it is left (Fig. 69). When these masses dissolve, the odd chromosome becomes visible as a round, smooth body (Figs. 67 and 68), which probably was concealed in the midst of the chromatic plate as far back as the contraction stage, but its presence was obscured by the similarity of its staining reaction to that of the other chromatin. As to the meaning of this deposition of chromatin on the nuclear membrane, it seems possible that it is basichromatin thrown out from the chromosome loops in the contraction stage, and that it takes no part in the further formation of the chromosomes, since it disappears before the next division. The only case at all similar which I can find in the literature is that of Gryllus campestris described by Voinov ('04). He claims that all the chromatin is gathered into the "corps nucleinien double," leaving the non-stainable achromatic substance spread through the nucleus, and that when the spireme forms, the chromatin is added to it again from this structure. He neglects the distinction between oxy and basichromatin, and thinks that when all

the stainable chromatin is aggregated into one body, there is no chromatin left elsewhere. The situation is much clearer if looked at from Conklin's point of view ('02): although the nucleus in the rest stage does not take basic stains, it still contains chromatin in the form of oxychromatin; this has the power of changing into basichromatin to form the chromosomes for division. The basichromatin masses of the rest stage, with the exception of the odd chromosome, which here again shows its individuality by a difference in behavior, are apparently rejected substances, which disappear without playing any further rôle in karyokinesis.

In the prophase, the odd chromosome lies close to the nuclear membrane as in the forms previously studied, and in the metaphase it has a somewhat eccentric position (Fig. 70). The chromosomes here are so nearly of the same size that it is impossible to trace any individuals from cell to cell; but the odd chromosome, by virtue of its position and its univalence, can be followed until the second spermatocytes are formed. Figs. 71 to 73 show its varying behavior in metaphase; it may either follow or precede the other chromosomes to the pole. This fact is shown also by the two anaphase figures, 74 and 75. The second spermatocyte equatorial plates show the two numbers of chromosomes 11 and 10 (Figs. 76 and 77), but the odd chromosome can no longer be distinguished from the others, either in metaphase (Fig. 78) or anaphase (Fig. 79). In all the spermatids (Fig. 80), there appears one large body (*n*) taking the basic stains, probably analogous to the body in the beetle spermatids called a chromatin nucleolus by Stevens ('06b). It is impossible to decide whether the odd chromosome in half the spermatids keeps its individuality as was observed in Entilia and Vanduzea, for all the chromatin stains deeply and in some stages is broken up into many separate masses (Fig. 80).

Ceresa bubalus

The only external difference between this species and the foregoing one is its greater size and the different angle of the prothoracic protuberances. The only difference in the spermatogenesis as can be seen by Figs. 81 to 92, is that the mass of rejected chromatin is not so conspicuous. In the bouquet stage (Fig. 81), the

plate is not nearly so large as in the same stage of Ceresa taurina (Fig. 63). Fig. 82 represents one of the most extreme cases of the growth stage.

Ceresa diceros

The shape and size of this species is about the same as in Ceresa bubalus, but the coloring is different, being brown and white, instead of uniform green. The spermatogenesis is practically the same, as Figs. 93 to 101 show, but a preparation from the testis of one could be distinguished from a preparation of the other, because the cells, chromosomes, and spindles of C. diceros are always smaller than those in C. bubalus.

Atymna castanea

This species was found on the chestnut trees exclusively, and was very abundant at the end of June and beginning of July. No spermatogonial plates in which the number of chromosomes could be counted were found. The odd chromosome appears in the rest stage as a large round body with a smooth contour and an affinity for basic stains (Fig. 102). In lateral view of the metaphase of the first spermatocyte division, it is apparent that it does not divide (Figs. 104 and 105), and in the anaphase it has the position usually characteristic of this order, between the plates of chromosomes, but nearer one pole than the other (Fig. 106). The number of chromosomes in the first spermatocyte is again 11 (Fig. 103), two of them constantly larger than the others (*a* and *b*). These two large chromosomes appear in all the second spermatocyte plates, whether they have 11 or 10 chromosomes (Figs. 107 and 108). All the spermatids contain a chromatin nucleolus (Fig. 111), as in the genus Ceresa. There being apparently no other basic-staining body in any of the spermatids, the odd chromosome in half of them must take part in the formation of the general reticulum like the other chromosomes.

Campylenchia curvata

Campylenchia curvata was found in sweepings from various weeds throughout July. The material showed all desirable stages.

Many spermatogonial plates were found, some of which it was possible to count. It seems that there must be one short period in the arrangement of the chromosomes into the plate, when they are spread further apart than at any other time. Judging from the behavior of the chromosomes of the first spermatocyte in coming into the equatorial plate, this more open stage must occur when the chromosomes are first drawn into a flat plate from their scattered position in prophase. Later as metakinesis begins and the mantle fibers pull from the two poles, the chromosomes are drawn closer together and the diameter of the plate becomes smaller. Fig. 112 shows a very clear spermatogonial plate, with 19 chromosomes. It is possible here to group the chromosomes into 9 pairs with one left over; only the two most distinct pairs are lettered, a_1 and a_2, long and slender, b_1 and b_2, a little shorter and thicker. The two chromosomes formed by the fusion of these pairs are designated by *a* and *b* in Fig. 114, the equatorial plate of the first spermatocyte, and in Figs. 117 and 118, the equatorial plates of the second spermatocytes. The number of chromosomes in the equatorial plates are what would be expected after finding 19 in the spermatogonia; 10 in the first spermatocytes, and 10 and 9, respectively, in the second. In the rest stages (Fig. 113), *x* appears as usual, but there are also present two other smaller bodies with the same staining reaction, m_1 and m_2. I have called them *m*-chromosomes, as they have all the characteristics of Wilson's *m*-chromosomes in the rest stage of the Hemiptera Heteroptera ('05c); they are of equal size and they take the basic stains like the odd chromosome. As unfortunately they are not enough smaller than some of the other chromosomes to be readily distinguished in the spermatogonial plate, or to be traced through the prophase of the first spermatocyte to the spindle, it is impossible to see whether they really represent one pair whose fusion has been delayed. The odd chromosome appears as usual in metaphase (Fig. 115) and anaphase (Fig. 116) of the first spermatocyte division, and as usual is not distinguishable in the metaphase (Fig. 119) or anaphase (Fig. 120) of the second division. In the spermatids, a basic-staining body appears in half the nuclei (Figs. 121 and 122), and so must here (as in Entilia and Vanduzea) represent the odd

chromosome, rather than the chromatin nucleolus of the other Membracidæ studied.

Enchenopa binotata

Enchenopa binotata was found throughout July at Cold Spring Harbor on the locust and wild cherry trees, on blackberry bushes and sometimes in general sweepings of weeds. Its spermatogenesis has been the most puzzling of any form studied and the following account is given tentatively, with the intention of going over the work as soon as more material can be obtained. The first facts to be noticed are that all the chromosomes appear as dumb-bells in the metakinesis of the first spermatocyte (Fig. 128), there is no lagging chromosome in the anaphase (Fig. 130), and all the second spermatocytes have 10 chromosomes (Fig. 131), the same number as the first spermatocytes. In iron hæmatoxylin preparations extracted to the same degree as in other material, no darkly-staining body appears in the rest stage, but in those extracted for a shorter time, a long twisted body appears against the pale spireme (Fig. 124). This can occasionally be traced into a stage where the spireme has segmented (Fig. 125), but never any further, as it does not assume a compact rounded shape until the other chromosomes become condensed. The question arises as to whether this body in the growth stage represents two spermatogonial chromosomes and consequently divides in both spermatocyte divisions as all bivalent chromosomes do; or whether it is univalent, analogous to most odd chromosomes in insects, but divides in the first spermatocyte division and not in the second, thus differing from all the other Hemiptera Homoptera studied and resembling most of the Heteroptera. There were a few spermatogonial plates in such a stage that it was possible to count the chromosomes, but these did not have the chromosomes as clearly spread apart as in most the other species studied. In five plates, 19 chromosomes were counted (Fig. 123) and in two, 20. One of those with 20 may, however, be deceptive; two of the chromosomes are much smaller than any in the other plates, the plate is at the surface of the section, and as x in Fig. 123 is V-shaped, it is possible that the bend of the V was cut off and the two small chro-

mosomes may really be but one. Other evidence for the univalence of one chromosome is its occasional appearance in early metaphase of the first spermatocytes when it has not yet assumed the dumb-bell shape (Fig. 129), and a few second spermatocyte metaphases where it apparently does not divide (Fig. 133). If it does not divide in the second spermatocyte division, the second spermatocyte spindle should always appear as it does in Fig. 133 rather than as in Fig. 132, unless the odd chromosome is usually in the center surrounded by the other chromosomes. That this probably is true is indicated by several cases like Fig. 135, the two anaphase groups of one second spermatocyte spindle, *a* having 9 chromosomes and *b* 10. There is a space in *a* corresponding to the chromosome marked *x* in *b*. This evidence is anything but satisfactory, but the possibility of such an exception to the general rule that the odd chromosome divides in the first spermatocyte division, is too interesting a fact to leave unmentioned. Here again one large chromosome in the first spermatocyte (Fig. 126) is represented by two in the spermatogonia (Fig. 123, a_1 and a_2), and by one in the second spermatocyte (Fig. 131, *a*). Fig. 127 shows an occasional first spermatocyte with 11 chromosomes, implying a delay in the fusion of one pair. Here we find the chromatin nucleolus in all the spermatids (Fig. 136).

Jassidæ

The testes of the Jassidæ are pale yellow in color, and therefore very easy to dissect out. The follicles are about three times as long as broad; this makes it easier to trace the development from stage to stage than in the Membracidæ. My material includes six species, four of them caught at Cold Spring Harbor in July, and the other two, Agallia sanguinolenta and Phlepsius irrotatus, at Bryn Mawr in October.

Chlorotettrix unicolor and C. vividus

This material was fixed and preserved as belonging to one species, but study of the sections showed two different reduced numbers of chromosomes, 11 and 9. This led to a careful com-

parison of my specimens with those in the collection at the Academy of Natural Sciences, Philadelphia. There proved to be two species, C. unicolor and C. vividus, in which the only marked difference is the width of head and thorax. Some of my specimens are slightly narrower than others, so I have probably mixed the two species, and cannot state whether the 9 chromosomes belong to C. unicolor or to C. vividus.

The resting spermatogonium has a reticulum of oxychromatin and linin and a plasmosome, which stains black in iron hæmatoxylin, but shows its achromatic nature in thionin (Fig. 137). There were no good spermatogonial plates in the material with the smaller number of chromosomes, but a lateral view of the spindle is shown in Fig. 138, and the anaphase in Fig. 139. The chromatin then passes into a contraction stage which is very dense, but contains several clear vacuoles (Fig. 140). This has a very different appearance from the contraction stage of the Membracidæ. A spireme stage follows where the chromatin again fills the nucleus and still stains deeply (Fig. 141). The odd chromosome is first visible in the rest stage (Fig. 142) where the chromatin stains least and is most scattered. It is closely applied to the nuclear membrane as was usually the case among the Membracidæ. The spireme splits longitudinally (Fig. 143), and then becomes segmented (Fig. 144). In all stages the odd chromosome can be distinguished by its small size. In the prophase of the first spermatocyte division, it can be recognized by its rounded contour; in the equatorial plate, by its eccentric position (Fig. 145); in the lateral view of the metaphase (Fig. 146), by its undivided condition; and in anaphase, by its lagging behind at one pole of the spindle (Fig. 147). In the equatorial plates of the second spermatocytes with 9 chromosomes, it can still be recognized by its small size (Fig. 149). As it divides in the second spermatocyte division, there is no indication of it in a lateral view of the metaphase (Fig. 150), or anaphase (Fig. 151). Two of the 9 chromosomes are larger than the others (*a* and *b* in Fig. 145), and they keep their individuality in the second spermatocyte (*a* and *b* in Figs. 148 and 149). In all the spermatids, there is one condensed body, which resembles the body called a chromatin nucleolus in

five species of the Membracidæ. In the early spermatid, this is the only condensed body distinguishable (Fig. 152), but later when the chromatin becomes more diffuse, it appears that half the spermatids have another smaller condensed body (Figs. 153 and 154), which is lacking in the other half. This must be the odd chromosome, observed in the same stages of three species of Membracidæ. In a still later stage, when the reticulum is arranged around a series of clear vacuoles, this difference is still to be observed; all the cells have the one large body, but only half have the small chromosome (Figs. 155 and 156). After this, both bodies disappear, the chromatin reticulum becomes slightly more condensed at first (Fig. 157), the nucleus then elongates but keeps the vacuoles (Fig. 158), and finally condenses into the head of the spermatozoön (Fig. 159). The acrosome is differentiated from cytoplasm at the apex of the head.

Fig. 160 is the spermatogonial plate of the species with the larger number of chromosomes. It contains 21 chromosomes, four larger than the others, not differing conspicuously in size among themselves (a_1, a_2, b_1, b_2). The first spermatocyte equatorial plate has 11 chromosomes, and they show the same size relation as those of the other species, two large ones and one small odd chromosome in an eccentric position (Fig. 161). This plate simply has two more chromosomes of intermediate size than the other. The second spermatocyte plates again show the two large chromosomes (Figs. 162 and 163), the total numbers being 11 and 10, instead of 9 and 8.

Diedrocephala coccinea

A few scattered individuals were found in July in general sweepings, but in August an abundance of material was obtained from the blackberry vines. The spermatogonial plates show 23 chromosomes, two larger than the others (a_1 and a_2 in Fig. 164). In the postsynapsis stage, the odd chromosome is not surrounded by the spireme, as has been the case in the forms described above, but it stands out distinctly by itself in the clear part of the nucleus (Fig. 165). In the rest stage, it is still of the same size and in the same position, although the nucleus grows much larger and the

chromatin becomes scattered and diffuse (Fig. 166). The first spermatocyte shows the odd chromosome as a medium-sized body, eccentric in the plate of 12 chromosomes (Fig. 167), and not dividing in metakinesis (Fig. 168). In anaphase, it lags behind the others (Fig. 169). The two large chromosomes of the spermatogonia have fused into a single large one in the first spermatocyte (*a* in Fig. 167), and this keeps its individuality in the second spermatocytes (*a* in Figs. 170 and 171). Half the second spermatocytes have 12 chromosomes, and half 11. The spermatids all have the chromatin nucleolus, and half of them the odd chromosome (Figs. 174 and 175), as in Chlorotettrix.

Diedrocephala mollipes

This species resembles Diedrocephala coccinea in shape, but not in color, being bright green instead of red and green striped. Its spermatogenesis is also similar (Figs. 176 to 185), but the cells and chromosomes are smaller (cf. Fig. 177 and 167). They both have the same number of chromosomes, 12, but Diedrocephala mollipes has no one chromosome markedly larger than the others. The spermatids have both a chromatin nucleolus and an odd chromosome.

Phlepsius irrotatus

The spermatogonial plate contains 15 chromosomes, two larger than the others (a_1 and a_2, Fig. 186). These are represented by *a* in the first spermatocyte (Fig. 188a) and also in the second spermatocytes (Figs. 191 and 192, *a*). The growth period shows the odd chromosome (*x*) as a round body with even contour (Fig. 187). The univalent chromosome *x* has the peculiarity here that it never comes to lie in a flat plate with the other chromosomes in the first spermatocyte division, as is indicated in Fig. 189. To get all 8 chromosomes, the equatorial plate must be drawn at two different foci (Figs. 188a and 188b). The odd chromosome always precedes the others to the pole (Fig. 190), never taking the lagging position characteristic of the species previously described. We have noted that this sometimes takes place in other forms (Vanduzea arcuata, and the three species of Ceresa), but Phlepsius is the first form

where this position is invariable. The second spermatocytes contain 8 and 7 chromosomes (Figs. 191 and 192). The spermatids all contain the chromatin nucleolus (Figs. 195, *n*, and 196, *n*) and half of them, an odd chromosome (Figs. 195 and 196, *x*).

Agallia sanguinolenta

No spermatogonial plates were found in this form. The odd chromosome appears as usual in the growth period (Fig. 197). There are 11 chromosomes in the first spermatocyte (Fig. 198), and 11 and 10 in the second (Figs. 200 and 201). The odd chromosome does not divide in the first spermatocyte metakinesis (Fig. 199), but passes to one pole after the other chromosomes in anaphase (Fig. 206). The spermatids all contain a chromatin nucleolus, and half of them, the odd chromosome (Figs. 203 and 204). Figs. 205 to 207 are drawn from aceto-carmine preparations at the same magnification as Figs. 197 to 204.

Cercopidæ

The testes of the Cercopidæ are situated near the posterior end of the abdomen. They are white in color, and each follicle is round, with a comparatively long duct joining it to the vas deferens. The material comprises four species, and the spermatogenesis of none of them resembles very closely that of the species studied by Stevens ('06b).

Clastoptera obtusa

This species was found on the alder at Cold Spring Harbor. The resting spermatogonium stains very lightly and has a plasmosome (Fig. 208). In preparing for division, the chromatin forms a spireme, which becomes more dense, and then segments (Fig. 209). There are 15 chromosomes in the spermatogonial equatorial plate, all of about the same size (Fig. 210). The division is longitudinal as usual (Figs. 211 and 212). After the telophase, the chromosomes soon become joined by linin connections (Fig. 213), form a compact spireme in early synapsis (Fig. 214), a dense mass in the contraction stage (Fig. 215) and a spireme loosely wound on itself in postsynapsis (Fig. 216). The odd chromosome

appears in the contraction stage distinct from the dense chromatin mass, and remains so in postsynapsis and the early growth stage (Fig. 217). It is from the first, a small, ovoid, smooth-contoured body, and still shows clearly when the spireme has segmented and the tetrads are forming (Fig. 218), and when the dumb-bells are formed (Fig. 219). It takes an eccentric position in the equatorial plate of the first spermatocyte (Fig. 220). It does not divide in the first spermatocyte division (Fig. 221), and is the last chromosome to reach the pole in the anaphase (Fig. 222). As there are 7 chromosomes, plus the odd one, in the first spermatocyte, so there are 8 in half the second spermatocytes (Fig. 223), and 7 in the others (Fig. 224). The odd chromosome behaves like the others in the second division (Figs. 225 and 226), and is not distinguishable in the spermatids, all of which have a chromatin nucleolus (Fig. 227). In the development of the spermatid, the chromatin reticulum first becomes massed on the side of the nucleus toward the axial filament (Fig. 228), and then forms a dense U, leaving the rest of the nucleus clear (Fig. 229). The nucleus then elongates, still leaving a clear space toward the apex (Fig. 230). The mature spermatozoön has a solid dense chromatic head (Fig. 231).

Aphrophora quadrangularis

This species was found on the grass and low bushes in July near Cold Spring Harbor. Originally a small quantity of material was collected and tried in aceto-carmine, as it was supposed to be the same species that Stevens ('06b) had found in Maine and described. But the reduced number of chromosomes proved to be 11 instead of 12, so material was fixed in Gilson and kept to be studied at a convenient time. The material was obtained from two distinct localities, but not kept separate. The sections showed follicles with 11 chromosomes and a few with 12. Whether this difference corresponds with the difference in locality it is unfortunately not possible to say. Another peculiarity is that the form with 12 chromosomes does not resemble, in some of its stages, the form with 12 chromosomes described by Stevens. The most important stages of the form with 11 chromosomes are shown in Figs. 232 to 242. There are 21 spermatogonial chromosomes (Fig. 232) and

11 and 10 second spermatocyte chromosomes (Figs. 238 and 239). The odd chromosome can be traced as an individual as far back as the contraction stage (Figs. 233, *x*, and 234, *x*). A plasmosome (*p*) also appears in the growth period, the thionin clearly bringing out the difference between the two. One of the 11 chromosomes is larger than the others, as is shown in Figs. 235, 238, 239. The odd chromosome does not divide in the first spermatocyte division (Figs. 236 and 237). The spermatids all contain a chromatin nucleolus (Fig. 242). A few stages of an individual with 12 chromosomes are shown in Figs. 243 to 248. This series much more nearly resembles that of the other form from Cold Spring Harbor with 11 chromosomes, than that of the form found in Maine with 12 chromosomes. The Maine form has no contraction stage (Stevens '06b, Figs. 240 to 249), while this form has a distinct one with the odd chromosome and the plasmosome outside of the spireme in the clear part of the nucleus (Fig. 243). The only possible conclusion seems to be that three species (so determined by the differences in spermatogenesis) have been up to this time grouped as one, and all called Aphrophora quadrangularis.

Aphrophora 4-notata

Aphrophora 4-notata is interesting especially in connection with Aphrophora quadrangularis, as being another case of difference of chromosome number within the same genus. Aphrophora 4-notata has 14 chromosomes for the reduced number (Fig. 250) and consequently 14 in half of the second spermatocytes (Fig. 253) and 13 in the other half (Fig. 254). The odd chromosome is present in the spireme stage (Fig. 249), and does not divide in the first spermatocyte division (Figs. 251 and 252).

Fulgoridæ

The testes of the Fulgoridæ are orange-colored and show through the thin white walls of the abdomen. The separate follicles are oblong. Of the four species in my material, three belong to the genus Pœciloptera, and one to the Amphiscepa, but according to the spermatogenesis, P. bivittata is much more like the Amphis-

cepa than like the other two species of Pœciloptera. P. septentrionalis and P. pruinosa were found on the nettle and the other two species came from sweeping low grasses. In this material, the cells and chromosomes are large and the achromatic structures especially well preserved. The material fixed in Flemming, and stained in thionin makes some of the clearest preparations included in this study.

Pœciloptera septentrionalis

The resting spermatogonia of this form are small and stain lightly (Fig. 256). In preparation for division, a spireme is formed, each granule of which splits longitudinally (Fig. 257). The chromatic part of the spireme segments, retaining the linin connections and also an indication of the longitudinal split (Fig. 258). There are 27 chromosomes in the spermatogonial plate, two longer than the others (a_1 and a_2 of Fig. 259). Fig. 260 shows distinctly that this division follows the preliminary longitudinal split. After the telophase, the chromosomes become more diffuse and join into a spireme (Fig. 262). This spireme contracts into a small dense ball at one side of the nucleus (Fig. 263), and then the cell goes through a long growth period in which the diameter is at least doubled. The odd chromosome appears as soon as the spireme becomes pale enough to conceal it no longer (Fig. 264). Then a pair of *m*-chromosomes appears and a small plasmosome (Fig. 265). The plasmosome and odd chromosome both increase in size, the latter having a vacuole in the center (Fig. 266). The odd chromosome has now attained its full size, but while the cell and nucleus continue to increase, the plasmosome keeps on growing (Fig. 267). Even though it is now larger than the odd chromosome, it stains scarcely at all, while the odd chromosome and the *m*-chromosomes stain a deep blue, thus demonstrating the valuable differentiating powers of thionin. In the next stage (Fig. 268) the odd chromosome and the plasmosome are unchanged, but the spireme stains more deeply and shows a longitudinal split. The *m*-chromosomes no longer appear, they have probably become indistinguishable from the other spireme segments. The plasmosome and odd chromosome still keep the same relative size in the pro-

phase, while the tetrads are forming (Fig. 269), the plasmosome sometimes not being dissolved until after the spindle is formed (Fig. 271). There are 14 chromosomes in the equatorial plate of the first spermatocyte (Fig. 270), one of them being marked by its eccentric position, another by its large size. This large chromosome keeps its individuality in all the second spermatocytes, those with 14 chromosomes (Fig. 273), and those with 13 (Fig. 274). The odd chromosome does not divide in the first spermatocyte division (Figs. 271 and 272), but does in the second (Figs. 275 and 276). The development of the spermatid in this family is very peculiar. The nucleus stains quite deeply, so that nothing more can be made out than that there seems to be one condensed body in each spermatid (Fig. 279a). The "Nebenkern" goes through a complicated development somewhat similar at first to that described by Baumgartner ('02). First delicate fibers are formed in it (Fig. 277), then it appears as a long coiled fiber in a clear space, surrounded by a definite membrane (Fig. 278). This space becomes separated by a partition into two tubes, each containing several shorter fibers (Figs. 279a and b). These tubes and fibers both become elongated (Fig. 280). The tubes grow still longer and smaller in diameter, and at the same time twist around each other in an irregular spiral (Fig. 281a). Cross sections through different portions of these twisted tubes indicate that they must also be constricted in places (Fig. 281b). They finally become flattened, presenting some such an appearance as in Fig. 282a, and in cross section as in Fig. 282b. In this species, the chromosomes in the female somatic cells could be counted, and proved to be 28 in number (Fig. 283), there being the same two long ones that appeared in the spermatogonial plate. The significance of the even number in the female, and the odd number in the male will be pointed out in the theoretical considerations.

Pœciloptera pruinosa

Pœciloptera pruinosa resembles the last described form externally in every character but color, being a grayish purple instead of a pale green. The principal stages are shown in Figs. 284 to 293, the only difference being that there are two large chromosomes

instead of one, in the first spermatocyte equatorial plate (Fig. 285) and also in the second spermatocyte plates (Figs. 288 and 289). The chromatin in the spermatid nucleus does not stain so deeply, and here it can be demonstrated that there is a chromatin nucleus in all of the spermatids (Figs. 292 and 293), and the odd chromosome besides in half of them (Fig. 292). Here also the female somatic chromosome number is 28. Fig. 294 shows some of the chromosomes overlapping each other, but they are really entirely separate from one another, lying at slightly different levels; it is a late prophase stage of an egg follicle cell before the chromosomes are drawn completely into one plane.

Amphiscepa bivittata

All this material came from larvæ. The different stages are shown in Figs. 295 to 304. The spermatogonial plates contain 25 chromosomes, two pairs of long ones, one pair longer than the other (Fig. 295). In the rest stage, there are no *m*-chromosomes, but two plasmosomes are present (Fig. 296). The first spermatocyte plate shows two large chromosomes, one larger than the other (Fig. 297), corresponding to the two large pairs of the spermatogonium. The plasmosomes here persist into the metaphase (Fig. 298). The odd chromosome is quite small (Figs. 297, *x*, 298, *x*, 299, *x*) and does not divide in the first division. Chromosomes *a* and *b* of the first spermatocyte retain their relative sizes in the second spermatocytes, both those containing 13 chromosomes (Fig. 300), and those with 12 (Fig. 301).

Pœciloptera bivittata

Pœciloptera bivittata very closely resembles the last described species, even to the number and relative sizes of its chromosomes (Figs. 305–313). It has two plasmosomes in the growth period, and one or both of these persist in a most remarkable fashion even to the anaphase of the second spermatocyte division (Fig. 312). The size of the chromosomes and cells is greater than in Amphiscepa bivittata.

THEORETICAL CONSIDERATIONS

Individuality of the Chromosomes

The theory of the individuality of the chromosomes was first proposed by Boveri ('88) as a result of his work on Ascaris. He found a constant number of chromosomes in each species, always half this number in the two maturation divisions, and the original number restored by fertilization. Every year adds to the number of species found conforming to these rules, and consequently making Boveri's theory more plausible. Beginning with Sutton's work in 1900, many species have been shown to give evidence of a more direct nature, and among these, the Hemiptera Homoptera can be classed. In the first place, it is a sign of individuality, when we are able to pick out one chromosome in every equatorial plate by some characteristic size, shape or position. This can be done for 14 out of the 22 species of Hemiptera Homoptera studied, the characteristic usually being the large size of the chromosome (see Pœciloptera septentrionalis, Figs. 270, 273, 274). Secondly, all evidence that supports Montgomery's hypothesis of the union of paternal and maternal chromosomes in synapsis necessarily supports the theory of the individuality of the chromosomes. In Pœciloptera septentrionalis, the large chromosome in the spermatocytes (Fig. 270) is represented in the spermatogonia (Fig. 259) by two large chromosomes. Half of the chromosomes in each spermatogonial plate must have come originally from the spermatozoön, and half from the egg. Only one large chromosome could be received from the spermatozoön, according to Fig. 270, therefore the other large one must have come from the egg. As these two large chromosomes, one paternal and one maternal, are represented by a single chromatic element in the spermatocyte, this must be formed by the union of a paternal with a maternal chromosome of the spermatogonium. Thus we see that the Hemiptera Homoptera are in accord with Montgomery's hypothesis of synapsis and reduction. In the third place, the behavior of the odd chromosome supports Boveri's theory. In the Hemiptera Homoptera, the odd chromosome can seldom be identified in the spermatogonia, but from the contraction stage to the

anaphase of the first spermatocyte, and sometimes to the metaphase of the second spermatocyte (Figs. 56 and 149) its individuality is marked. It takes the basic stains when the rest of the chromatin takes acid stains; it frequently has a smooth round contour in the early prophase, when the other chromosomes are irregular rods or tetrads; it usually is closely applied to the nuclear membrane until that is dissolved, and then keeps an eccentric position in the first spermatocyte equatorial plate; it does not divide in this division, and either precedes or follows the other chromosomes to the pole. In Vanduzea arcuata (Fig. 56), where it is intermediate in size, and in Chlorotettrix (Fig. 149), where it is the smallest chromosome, its individuality is still marked in the second spermatocyte. Finally the facts that have brought about the dropping of the old discussion about prereduction and postreduction, speak for the individuality of the chromosomes, in that they show the essential point of reduction to be the separation of each maternal chromosome from its paternal mate, and their distribution to different spermatozoa. The uselessness of insisting on prereduction or postreduction is shown within the order Hemiptera, where the odd chromosome may divide in either division; in the Heteroptera, it usually divides in the first, while in the Homoptera, the usual place of division is the second spermatocyte, but Archimerus and Banassa are exceptions in the former and Enchenopa in the latter.

Value of the Number of Chromosomes in Taxonomy and Evolution

McClung ('05) states that for Orthoptera, a certain number of chromosomes is characteristic for each family, the chromosome grouping marking the genus, and the relative size of the chromosomes indicating the species. Unfortunately this is not true for the Hemiptera Homoptera as the number varies within the family and even within the genus, being constant for the species only. The case of Aphrophora quadrangularis may make this doubtful, although it seems more probable that two or three species have previously been included under one name, than that in the same species, the reduced number should be sometimes 12 and sometimes 11, which would not accord with the simplest laws of heredity.

Montgomery has for many years endeavored to determine the stage of evolution by the number of chromosomes that a species possesses, those having few being considered higher in the scale than those with many. The chromatin nucleoli were supposed to be degenerating chromosomes as a species evolves to a higher form. But he has recently collected data from all the scattered literature, tabulated the number of chromosomes and the species, and finds that there is no such correlation ('06b). In the Hemiptera Homoptera there is no reason for considering Vanduzea arcuata, with 9 chromosomes, more highly evolved than Entilia sinuata, with 11, or Phlepsius irrotatus, with 8, more so than Pœciloptera septentrionalis, with 14.

Sex Determination

We have seen in the historical review of the work on tracheate spermatogenesis, that the most recent and reliable work all points to a dimorphism of the spermatozoa in the forms with an odd chromosome or an unequal pair of chromosomes. McClung was the first to suggest that the one characteristic that most generally divides the animal kingdom into two equal classes is sex, and that therefore, the dimorphism of sex and of spermatozoa may be causally connected. There is need of careful statistical work on the proportion of males and females among different species of insects. In general collecting, however, one gets an impression of equality in numbers. McClung's theory was a brilliant guess, which the work of Stevens and Wilson has substantiated.

The Hemiptera Homoptera furnish additional evidence for this theory. Females of many of the species were sectioned for oögonial and somatic equatorial plates. Only two furnished the desired stages, Pœciloptera septentrionalis and Pœciloptera pruinosa. In both the spermatogonial number is 27, the spermatozoa possessing 13 and 14 chromosomes, and the female somatic number is 28. Stevens and Wilson have shown that there is no difference between the somatic number and the unreduced number in the germ cells; in the female, both numbers are even, in the male, both are odd (or even, when a small chromosome is included). As the female somatic number in Pœciloptera is even, the oögonial

number must also be even, and all the maturated eggs necessarily possess the same number of chromosomes, 14. Applying Wilson's ('06b) formula for sex determination to the Pœciloptera, we have the following:

I Egg (14 chromosomes) + Spermatozoön (14 chromosomes) = Female (28 chromosomes).

II Egg (14 chromosomes) + Spermatozoön (13 chromosomes) = Male (27 chromosomes).

Here again it is possible to apply Castle's ('00) theory of sex as a Mendelian character, which has been so fully elaborated and applied to the case of the odd chromosome by Wilson. It involves the assumption of two kinds of eggs, male and female, as well as the two kinds of spermatozoa which are actually to be observed. It also involves the assumption of selective fertilization: an egg bearing the female determinant must be fertilized by a spermatozoön with the male determinant, while an egg bearing the male determinant must be fertilized by a spermatozoön with the female determinant. In case II of the above formula when the egg is fertilized by the spermatozoön without the odd chromosome, the sex determinant must be introduced by the egg; and as in this case, a male is produced, the eggs fertilized by a spermatozoön without an odd chromosome must bear the male determinant, and the chromosome which has disappeared in the males must be the one with the female character. So in case I, where the egg is fertilized by the spermatozoön with the odd chromosome, the spermatozoön must bear the male character and the egg the female; as this combination always results in a female, it is necessary to assume that the male character is recessive and the female dominant. The above formulæ can be extended to show these assumptions and will read thus:

I ♀ Egg (14 chromosomes) + (♂) Spermatozoön (14 chromosomes) = ♀ (♂) Female (28 chromosomes).

II (♂) Egg (14 chromosomes) + (o) Spermatozoön (13 chromosomes) = (♂) (o) Male (27 chromosomes).

This is the part of Wilson's theory that deals with the case presented by Pœciloptera and presumably the other Hemiptera Homoptera. The facts as far as they go are not at variance with the theory.

SUMMARY

1 An odd chromosome is present in the spermatogenesis of 22 species of the Hemiptera Homoptera, as shown in each case by some or all of the following facts:

a The spermatogonia have an uneven number of chromosomes.

b A dense body takes basic stains in the growth period.

c One chromosome stands in an eccentric position in the first spermatocyte equatorial plate.

d In the metaphase of the first spermatocyte division, one chromosome does not divide, and has half the valence of the others, as shown by its spherical shape when the others are like dumbbells.

e In anaphase of the first spermatocyte division, one chromosome at one pole behaves differently from the others, either preceding or lagging behind.

f Half of the equatorial plates of the second spermatocytes contain the same number of chromosomes as those of the first spermatocytes, but half contain one less.

g Half of the spermatids contain a condensed body, taking basic stains, which is the odd chromosome.

2 The odd chromosome shows certain variations in behavior, either individual or specific.

a In the anaphase of the division where it does not divide, in some cells it may precede the other chromosomes to the poles, while in others it lags behind them.

This individual variation is a characteristic of certain species, the three species of Ceresa and Vanduzea arcuata, while most of the species studied have the odd chromosome always lagging behind, and Phlepsius irrotatus has it always preceding the others.

b In Enchenopa binotata, it divides in the first division, and in the second division, where it does not divide, it neither precedes nor lags behind the others.

c The shape of the odd chromosome in the growth period varies. It may be always spherical or ovoid with a smooth contour, as in the Fulgoridæ, Cercopidæ, Jassidæ, and some of the Membracidæ. It may be long and uneven in contour as in Vanduzea arcuata and Enchenopa binotata.

It may pass through both forms in different stages, as in Entilia sinuata.

3 In the spermatids of 19 species; that is, all except three of the Membracidæ, there is a chromatin nucleolus in all of the spermatids entirely independent of the odd chromosome. In seven of these species, the odd chromosome is present also in half of the spermatids, in others there is no indication of it. In the three Membracidæ without the chromatin nucleolus, Entilia sinuata, Vanduzea arcuata, and Campylenchia curvata, the odd chromosome is present in half of the spermatids.

4 In the genus Ceresa, in the contraction stage some of the basichromatin is thrown out from the chromatin loops and persists through the growth period as a chromatin deposition on the nuclear membrane and finally dissolves without apparently taking part in the formation of the chromosomes for the first spermatocyte division.

5 In three species, Campylenchia curvata, Pœciloptera septentrionalis, and Pœciloptera pruinosa, a pair of *m*-chromosomes remain condensed in the growth period.

6 The number of chromosomes has no significance for grouping species into families. In reduced number,

in the Membracidæ,	5 species have	11 chromosomes
	2 species have	10 chromosomes
	1 species has	9 chromosomes
in the Jassidæ,	2 species have	12 chromosomes
	2 species have	11 chromosomes
	1 species has	9 chromosomes
	1 species has	8 chromosomes
in the Cercopidæ,	1 species has	14 chromosomes
	1 species has	12 chromosomes
	1 species has	11 chromosomes
	1 species has	8 chromosomes
in the Fulgoridæ,	2 species have	14 chromosomes
	2 species have	13 chromosomes

7 The number of chromosomes has no significance for grouping species into genera.

Chlorotettrix unicolor,	11 chromosomes
Chlorotettrix vividus,	9 chromosomes
Aphrophora quadrangularis,	11 or 12 chromosomes
Aphrophora 4-notata,	14 chromosomes
Pœciloptera septentrionalis,	14 chromosomes
Pœciloptera bivittata,	13 chromosomes

8 The number of chromosomes is constant for each species. In the case of Aphrophora quadrangularis, where there have been found both 11 and 12 chromosomes, probably two species are present, which have not been separated in classification.

9 The only points in the spermatogenesis in which all of the species of one family resemble each other more closely than they do the species of the other families are the appearance of some of the growth stages and the transformation of the spermatid into the spermatozoön.

10 In fourteen of the species studied, the individuality of certain chromosomes can be traced from the spermatogonium to the second spermatocyte, a pair of similar chromosomes in the spermatogonium bearing the same size relation to the other chromosomes of the equatorial plate as a single chromosome bears to the others in the first and second spermatocyte plates. In all the species, the odd chromosome can be traced as keeping its individuality from the growth period to the anaphase of the first spermatocyte division, in Chlorotettrix and Vanduzea arcuata to the metaphase of the second spermatocyte division, and in Enchenopa binotata, from the spermatogonial plate to the telophase of the second spermatocyte division.

11 In all 22 species, there is a dimorphism of the spermatozoa, which probably corresponds to the natural dimorphism of sex.

12 Two species of Fulgoridæ in which the female somatic number of chromosomes is 28, while the spermatogonial number is 27, furnish further proof for the theory of sex determination advanced by McClung, Wilson and Stevens.

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DESCRIPTION OF PLATES.

The figures were drawn with the aid of the Zeiss-Abbe drawing camera, No. 111. Figs. 1–46 were drawn with a Leitz oil immersion obj. $\frac{1}{12}$ and a Zeiss compensating oc. 12, Figs. 47–313 with a Zeiss apochromatic oil immersion obj. 2 mm., oc. 12. They have been reduced one-third, giving a magnification of about 1000 diameters.

Abbreviations Used on Plates

a_1 and a_2 = one pair of spermatogonial chromosomes.

a = a bivalent primary spermatocyte chromosome representing a_1 and a_2.

b_1 and b_2 = one pair of spermatogonial chromosomes.

b = a bivalent primary spermatocyte chromosome representing b_1 and b_2.

m_1 and m_2 = a pair of m-chromosomes.

n = chromatin nucleolus.

p, p_1, p_2 = plasmosomes.

x = odd chromosome.

Plate I

Entilia sinuata (*Family Membracidæ*)

Fig. 1 Spermatogonial rest stage.
Fig. 2 Spermatogonial spireme.
Fig. 3 Spermatogonium, segmentation of the spireme, each segment longitudinally split.
Fig. 4 Spermatogonium, condensation of the segments of the spireme.
Fig. 5 Spermatogonial equatorial plate, 21 chromosomes.
Fig. 6 Spermatogonial metaphase.
Fig. 7 Spermatogonial anaphase.
Fig. 8 Spermatogonial telophase, formation of nuclear membrane.
Fig. 9 Spermatogonial telophase, polar view.
Fig. 10 First spermatocyte, contraction stage.
Fig. 11 First spermatocyte, early postsynapsis stage.
Fig. 12 First spermatocyte, late postsynapsis, fine spireme.
Fig. 13 First spermatocyte, coarse spireme.
Fig. 14 First spermatocyte, rest stage.
Fig. 15 First spermatocyte, split spireme.
Fig. 16 First spermatocyte, spireme divided into 11 split segments.
Figs. 17–19 First spermatocyte, early prophase, tetrad formation.
Fig. 20 First spermatocyte, late prophase, dumb-bell formation.
Fig. 21 First spermatocyte, equatorial plate, 11 chromosomes.
Fig. 22 First spermatocyte, metaphase, chromosomes still tetrads.
Figs. 23, 24 First spermatocyte, metaphase.
Figs. 25, 26 First spermatocyte, anaphase, centrosomes divided for the second division.
Fig. 27 First spermatocyte, telophase.
Fig. 28 First spermatocyte, telophase, polar view.
Fig. 29 Rearrangement of chromosomes for the second spermatocyte division.
Fig. 30 Second spermatocyte, equatorial plate, 11 chromosomes.

MEMBRACIDÆ

A. M. B. *del.*

Plate II

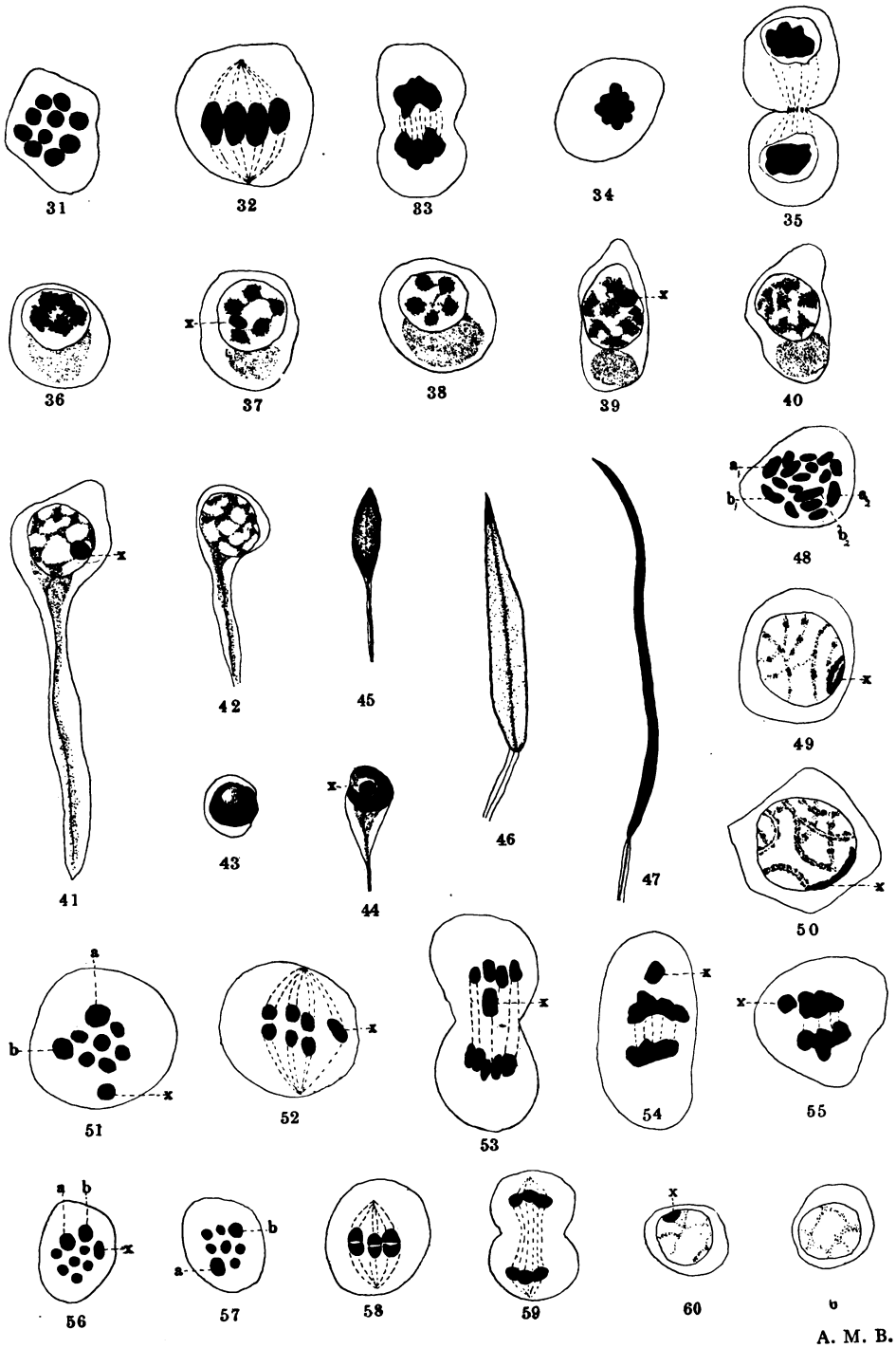
Entilia sinuata (*continued*)

Fig. 31 Second spermatocyte, equatorial plate, 10 chromosomes.
Fig. 32 Second spermatocyte, metaphase.
Fig. 33 Second spermatocyte, anaphase.
Fig. 34 Second spermatocyte, anaphase, polar view.
Fig. 35 Second spermatocyte, telophase.
Fig. 36 Spermatid, first stage.
Figs. 37, 38 Spermatids, second stage, half with x, half without.
Figs. 39, 40 Spermatids, third stage, half contain x, half do not.
Figs. 41, 42 Spermatids, formation of axial filament, half contain x, half do not.
Figs. 43, 44 Spermatids, condensation of the chromatin, half contain x, half do not.
Figs. 45, 46 Spermatids, later stages.
Fig. 47 Mature spermatozoön.

Vanduzea arcuata (*Family Membracidæ*)

Fig. 48 Spermatogonial equatorial plate, 17 chromosomes.
Figs. 49, 50 First spermatocyte, growth period.
Fig. 51 First spermatocyte, equatorial plate, 9 chromosomes.
Fig. 52 First spermatocyte, metaphase.
Figs. 53–55 First spermatocyte, anaphase.
Figs. 56, 57 Second spermatocytes, equatorial plates, containing 9 and 8 chromosomes, respectively.
Fig. 58 Second spermatocyte, metaphase.
Fig. 59 Second spermatocyte, anaphase.
Figs. 60, 61 Spermatids, half contain x, half do not.

SPERMATOGENESIS
Alice M. Boring



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MEMBRACIDÆ

Plate III

Ceresa taurina (*Family Membracidæ*)

Figs. 62, 63 First spermatocyte contraction stage, a mass of rejected basichromatin at the base of the loops.

Figs. 64–66 First spermatocyte, rest stage, showing rejected basichromatin.

Fig. 67 First spermatocyte, rest stage, showing x in the midst of the rejected chromatin.

Fig. 68 First spermatocyte, split spireme stage. Most of the rejected chromatin has dissolved, showing x plainly.

Fig. 69 First spermatocyte, prophase.

Fig. 70 First spermatocyte, equatorial plate, 11 chromosomes.

Figs. 71–73 First spermatocyte, metaphase.

Figs. 74, 75 First spermatocyte, anaphase.

Figs. 76, 77 Second spermatocyte, equatorial plates, containing 11 and 10 chromosomes, respectively.

Fig. 78 Second spermatocyte, metaphase.

Fig. 79 Second spermatocyte, anaphase.

Fig. 80 Spermatid, with chromatin nucleolus.

Ceresa bubalus (*Family Membracidæ*)

Fig. 81 First spermatocyte, synapsis stage, showing rejected chromatin.

Fig. 82 First spermatocyte, rest stage, showing rejected chromatin.

Fig. 83 First spermatocyte, equatorial plate, 11 chromosomes.

Figs. 84, 85 First spermatocytes, metaphase.

Figs. 86, 87 First spermatocytes, anaphase.

Figs. 88, 89 Second spermatocytes, equatorial plates, containing 11 and 10 chromosomes, respectively.

Fig. 90 Second spermatocyte, metaphase.

Fig. 91 Second spermatocyte, anaphase.

Fig. 92 Spermatid, with chromatin nucleolus.

Ceresa diceros (*Family Membracidæ*)

Fig. 93 First spermatocyte, rest stage, showing rejected chromatin.

Fig. 94 First spermatocyte, equatorial plate, 11 chromosomes.

Fig. 95 First spermatocyte, metaphase.

Fig. 96 First spermatocyte, anaphase.

Figs. 97, 98 Second spermatocytes, equatorial plates, containing 11 and 10 chromosomes, respectively.

Fig. 99 Second spermatocyte, metaphase.

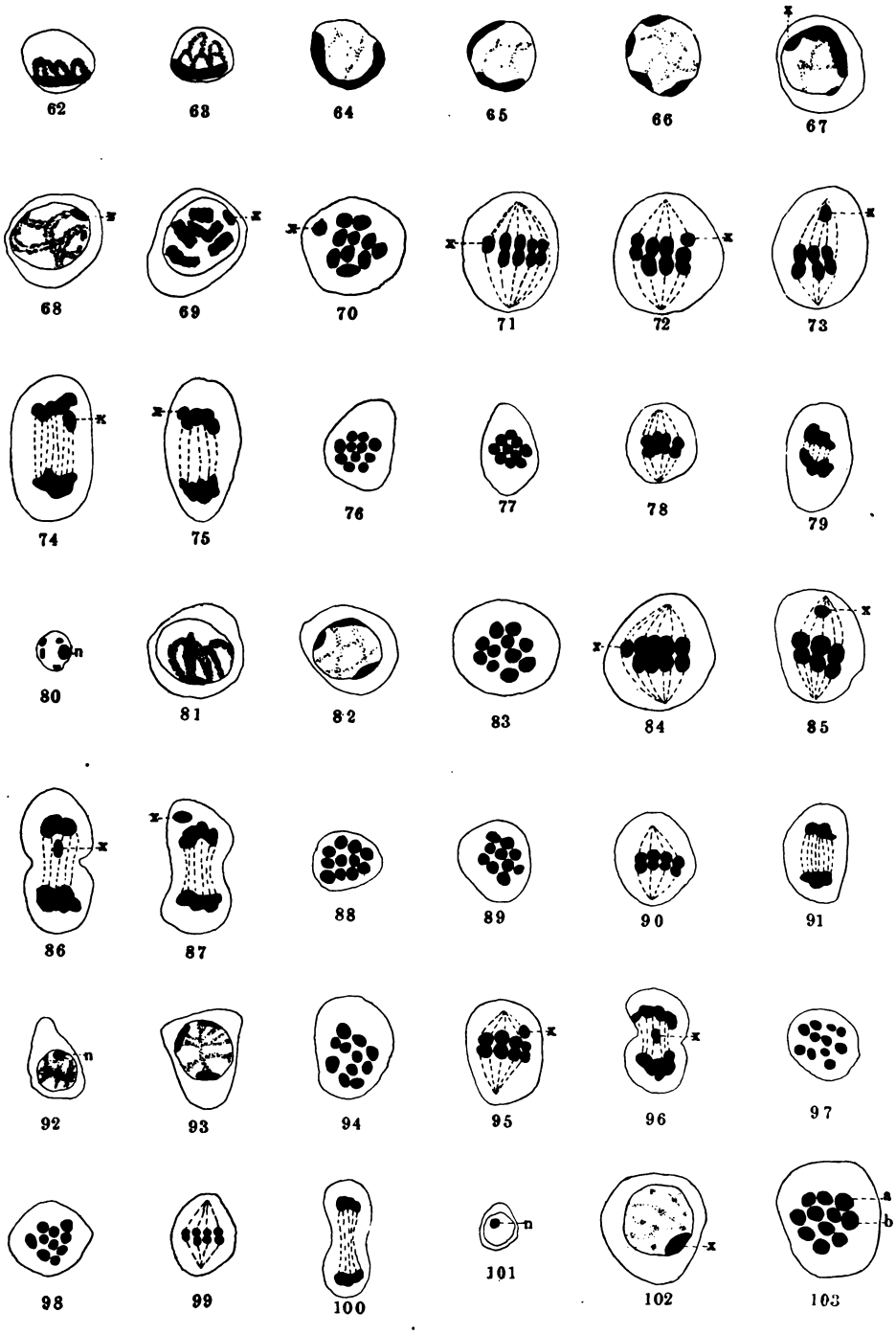
Fig. 100 Second spermatocyte, anaphase.

Fig. 101 Spermatid with chromatin nucleolus.

Atymna castanea (*Family Membracidæ*)

Fig. 102 First spermatocyte, rest stage.

Fig. 103 First spermatocyte, equatorial plate, 11 chromosomes.



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MEMBRACIDÆ

Plate IV

Atymna castanea (*continued*)

Figs. 104, 105 First spermatocyte, metaphase.

Fig. 106 First spermatocyte, anaphase.

Figs. 107, 108 Second spermatocytes, equatorial plates, containing 11 and 10 chromosomes, respectively.

Fig. 109 Second spermatocyte, metaphase.

Fig. 110 Second spermatocyte, anaphase.

Fig. 111 Spermatid, with chromatin nucleolus.

Campylenchia curvata (*Family Membracidæ*)

Fig. 112 Spermatogonial equatorial plate, 19 chromosomes.

Fig. 113 First spermatocyte, rest stage.

Fig. 114 First spermatocyte, equatorial plate, 10 chromosomes.

Fig. 115 First spermatocyte, metaphase.

Fig. 116 First spermatocyte, anaphase.

Figs. 117, 118 Second spermatocytes, equatorial plates, containing 10 and 9 chromosomes, respectively.

Fig. 119 Second spermatocyte, metaphase.

Fig. 120 Second spermatocyte, anaphase.

Figs. 121, 122 Spermatids, half with x, half without.

Enchenopa binotata (*Family Membracidæ*)

Fig. 123 Spermatogonial equatorial plate, 19 chromosomes.

Fig. 124 First spermatocyte, spireme stage.

Fig. 125 First spermatocyte, early prophase.

Fig. 126 First spermatocyte, equatorial plate, 10 chromosomes.

Fig. 127 First spermatocyte, equatorial plate, 11 chromosomes, occasionally found.

Figs. 128, 129 First spermatocytes, metaphase.

Fig. 130 First spermatocyte, anaphase.

Fig. 131 Second spermatocyte, equatorial plate, 10 chromosomes.

Figs. 132, 133 Second spermatocytes, metaphase.

Fig. 133 x does not divide in this division.

Fig. 134 Second spermatocyte, anaphase.

Fig. 135a and b Second spermatocyte anaphase, two plates from the same spindle, 9 chromosomes in one, 10 in the other.

Fig. 136 Spermatid, with chromatin nucleolus.

Chlorotettrix unicolor and Chlorotettrix vividus Family Jassidæ)

Fig. 137 Spermatogonial rest stage.

Fig. 138 Spermatogonial metaphase.

Fig. 139 Spermatogonial anaphase.

Fig. 140 First spermatocyte, contraction stage.

Fig. 141 First spermatocyte, spireme stage.

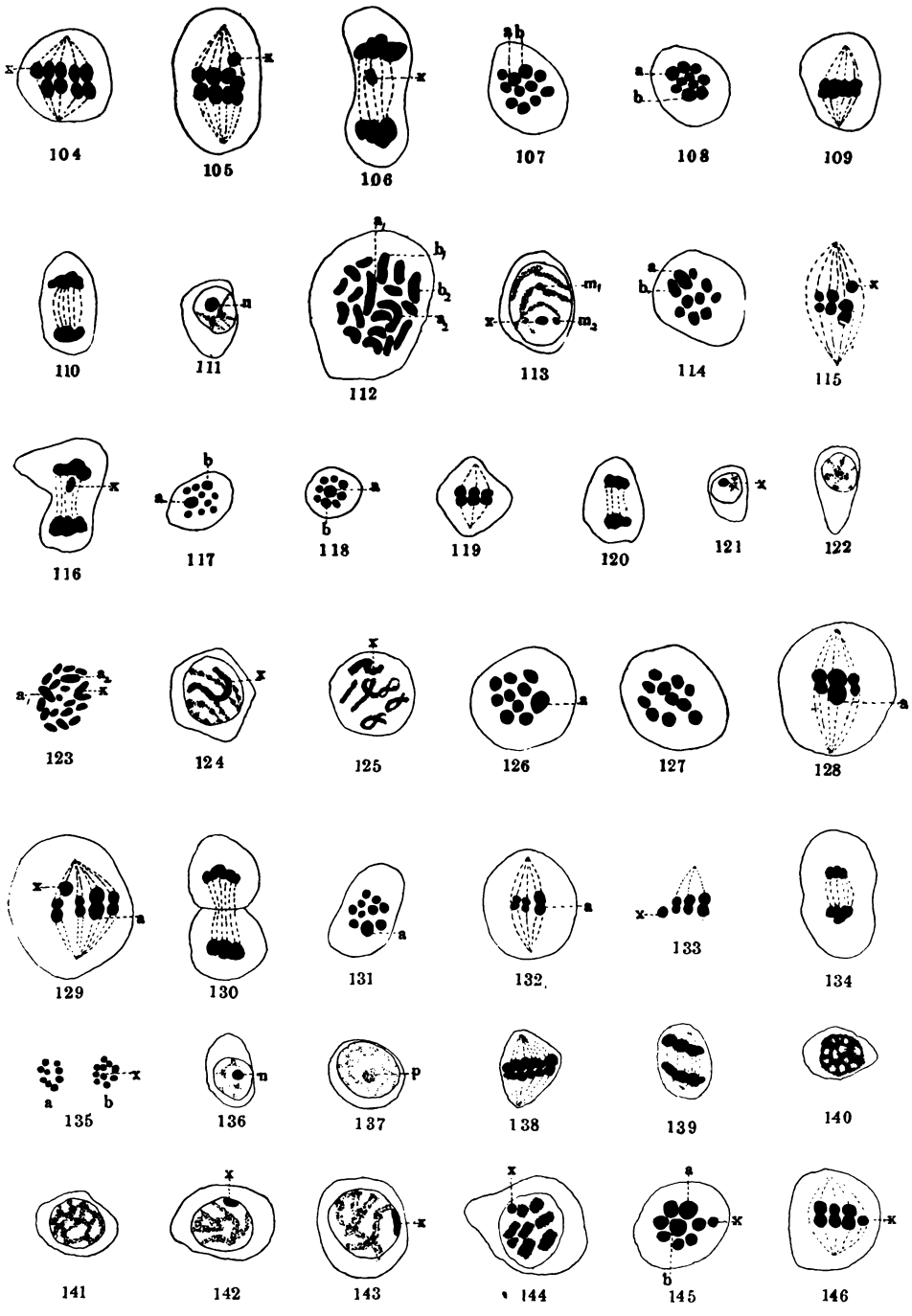
Fig. 142 First spermatocyte, rest stage.

Fig. 143 First spermatocyte, split spireme stage.

Fig. 144 First spermatocyte, prophase.

Fig. 145 First spermatocyte, equatorial plate, 9 chromosomes.

Fig. 146 First spermatocyte, metaphase.



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MEMBRACIDÆ AND JASSIDÆ

Plate V

Chlorotettrix unicolor and Chlorotettrix viridus (continued)

Fig. 147 First spermatocyte, anaphase.

Figs. 148, 149 Second spermatocytes, equatorial plates, containing 8 and 9 chromosomes, respectively.

Fig. 150 Second spermatocyte, metaphase.

Fig. 151 Second spermatocyte, anaphase.

Fig. 152 Spermatid, first stage.

Figs. 153, 154 Spermatid, second stage, half with x, half without.

Figs. 155, 156 Spermatid, third stage, half with x, half without.

Figs. 157, 158 Late spermatid stages.

Fig. 159 Head of mature spermatozoön.

Fig. 160 Spermatogonial equatorial plate, 21 chromosomes.

Fig. 161 First spermatocyte equatorial plate, 11 chromosomes.

Figs. 162, 163 Second spermatocytes, equatorial plates, containing 11 and 10 chromosomes, respectively.

Diedrocephala coccinea (Family Jassidæ)

Fig. 164 Spermatogonial equatorial plate, 23 chromosomes.

Fig. 165 First spermatocyte, postsynapsis stage.

Fig. 166 First spermatocyte, rest stage.

Fig. 167 First spermatocyte, equatorial plate, 12 chromosomes.

Fig. 168 First spermatocyte, metaphase.

Fig. 169 First spermatocyte, anaphase.

Figs. 170, 171 Second spermatocytes, equatorial plates, containing 12 and 11 chromosomes, respectively.

Fig. 172 Second spermatocyte, metaphase.

Fig. 173 Second spermatocyte, anaphase.

Figs. 174, 175 Spermatids, half without x, half with.

Diedrocephala mollipes (Family Jassidæ)

Fig. 176 First spermatocyte, rest stage.

Fig. 177 First spermatocyte, equatorial plate, 12 chromosomes.

Fig. 178 First spermatocyte, metaphase.

Fig. 179 First spermatocyte, anaphase.

Figs. 180, 181 Second spermatocytes, equatorial plates, containing 12 and 11 chromosomes, respectively.

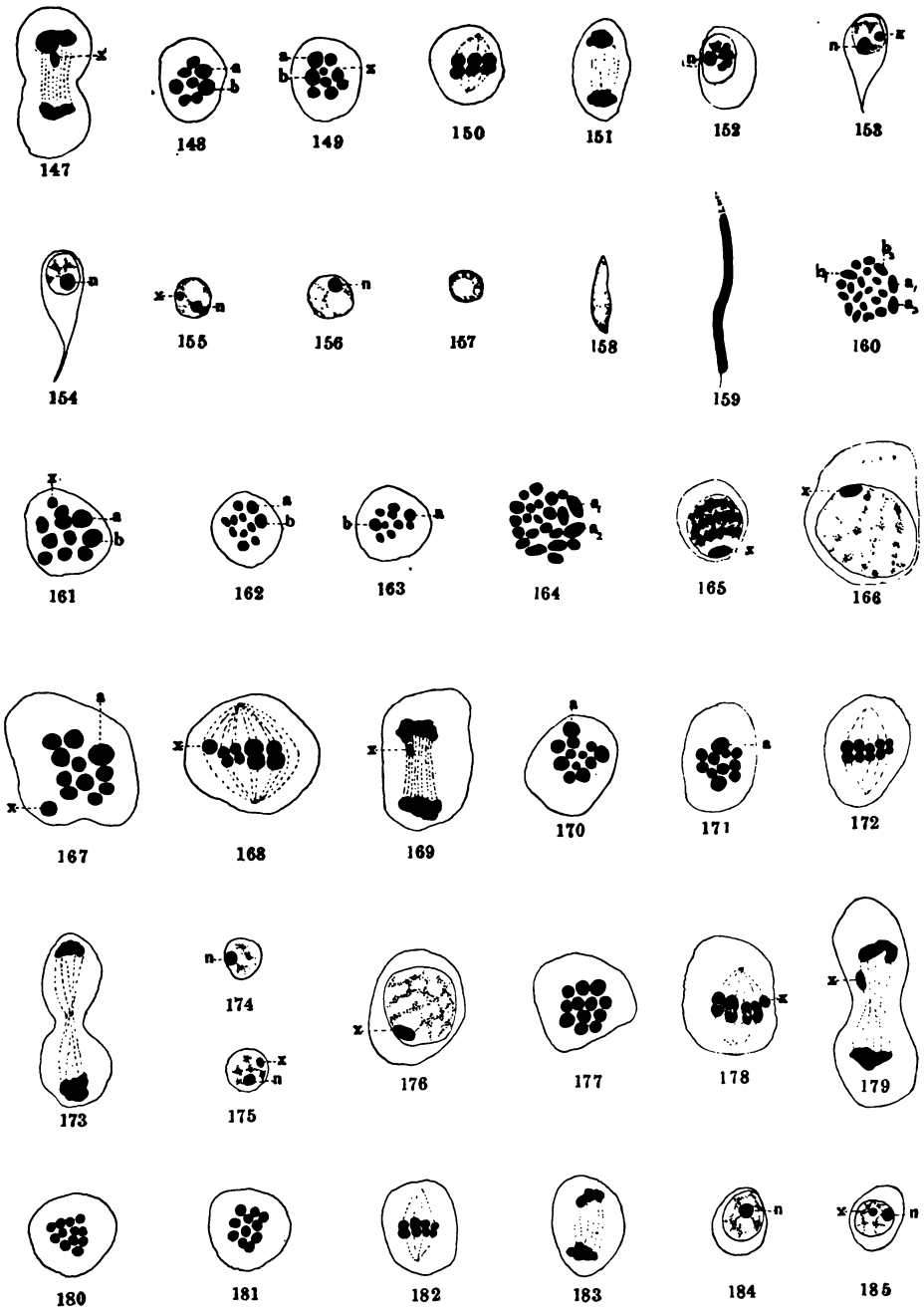
Fig. 182 Second spermatocyte, metaphase.

Fig. 183 Second spermatocyte, anaphase.

Figs. 184, 185 Spermatids, half without x, half with.

SPERMATOGENESIS
Alice M. Boring

PLATE IV



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JASSIDÆ

Plate VI

Phlepsius irrotatus (*Family Jassidæ*)

Fig. 186 Spermatogonial equatorial plate, 15 chromosomes.

Fig. 187 First spermatocyte, rest stage.

Fig. 188a and b First spermatocyte, equatorial plate, and the odd chromosome *x*.

Fig. 189 First spermatocyte, metaphase.

Fig. 190 First spermatocyte anaphase.

Figs. 191, 192 Second spermatocytes, equatorial plates, containing 8 and 7 chromosomes, respectively.

Fig. 193 Second spermatocyte, metaphase.

Fig. 194 Second spermatocyte, anaphase.

Figs. 195, 196 Spermatids, half without *x*, half with.

Agallia sanguinolenta (*Family Jassidæ*)

Fig. 197 First spermatocyte, spireme stage.

Fig. 198 First spermatocyte, equatorial plate, 11 chromosomes.

Fig. 199 First spermatocyte, metaphase.

Figs. 200, 201 Second spermatocytes, equatorial plates, containing 11 and 10 chromosomes, respectively.

Fig. 202 Second spermatocyte, early anaphase.

Figs. 203, 204 Spermatids, half without *x*, half with.

Fig. 205 First spermatocyte, equatorial plate, aceto-carmine preparation.

Fig. 206 First spermatocyte, anaphase, aceto-carmine preparation.

Fig. 207 Second spermatocyte, equatorial plate, aceto-carmine preparation.

Clastoptera obtusa (*Family Cercopidæ*)

Fig. 208 Spermatogonial rest stage.

Fig. 209 Spermatogonial prophase.

Fig. 210 Spermatogonial equatorial plate, 15 chromosomes.

Fig. 211 Spermatogonial metaphase.

Fig. 212 Spermatogonial anaphase.

Figs. 213, 214 First spermatocyte, early synapsis.

Fig. 215 First spermatocyte, contraction stage.

Fig. 216 First spermatocyte, postsynapsis stage.

Fig. 217 First spermatocyte, spireme stage.

Fig. 218 First spermatocyte, early prophase, tetrad formation.

Fig. 219 First spermatocyte, prophase, dumb-bell formation.

Fig. 220 First spermatocyte, equatorial plate, 8 chromosomes.

Fig. 221 First spermatocyte, metaphase.

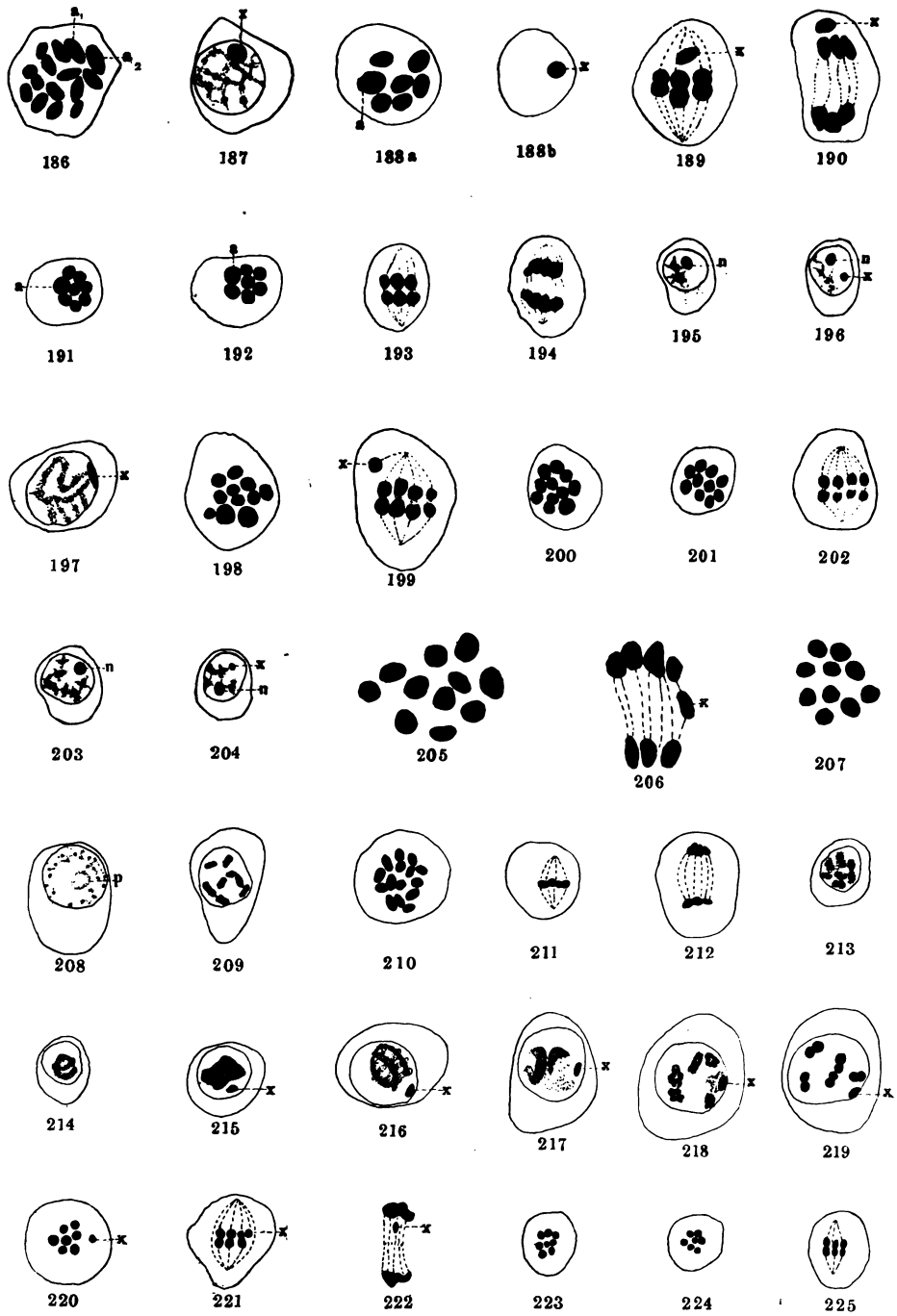
Fig. 222 First spermatocyte, anaphase.

Figs. 223, 224 Second spermatocytes, equatorial plates containing 8 and 7 chromosomes, respectively.

Fig. 225 Second spermatocyte, metaphase.

SPERMATOGENESIS
Alice M. Boring

PLATE VI



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JASSIDÆ AND CERCOPIDÆ

Plate VII

Clastoptera obtusa (*Continued*)

Fig. 226 Second spermatocyte, anaphase.

Fig. 227 Early spermatid, with chromatin nucleolus.

Fig. 228 Spermatid, formation of axial filament.

Figs. 229, 230 Later spermatids.

Fig. 231 Mature spermatozoön.

Aphrophora quadrangularis with 11 chromosomes (*Family Cercopidæ*)

Fig. 232 Spermatogonial equatorial plate, 21 chromosomes.

Fig. 233 First spermatocyte, contraction stage.

Fig. 234 First spermatocyte, spireme stage.

Fig. 235 First spermatocyte, equatorial plate, 11 chromosomes.

Fig. 236 First spermatocyte, metaphase.

Fig. 237 First spermatocyte, anaphase.

Figs. 238, 239 Second spermatocytes, equatorial plates, containing 11 and 10 chromosomes, respectively.

Fig. 240 Second spermatocyte, metaphase.

Fig. 241 Second spermatocyte, anaphase.

Fig. 242 Spermatid, with chromatin nucleolus.

Aphrophora quadrangularis with 12 chromosomes (*Family Cercopidæ*)

Fig. 243 First spermatocyte, contraction stage.

Fig. 244 First spermatocyte, equatorial plate, 12 chromosomes.

Fig. 245 First spermatocyte, metaphase.

Fig. 246 First spermatocyte, anaphase.

Fig. 247 Second spermatocyte, equatorial plate, 12 chromosomes.

Fig. 248 Second spermatocyte, anaphase.

Aphrophora 4-notata (*Family Cercopidæ*)

Fig. 249 First spermatocyte, spireme stage.

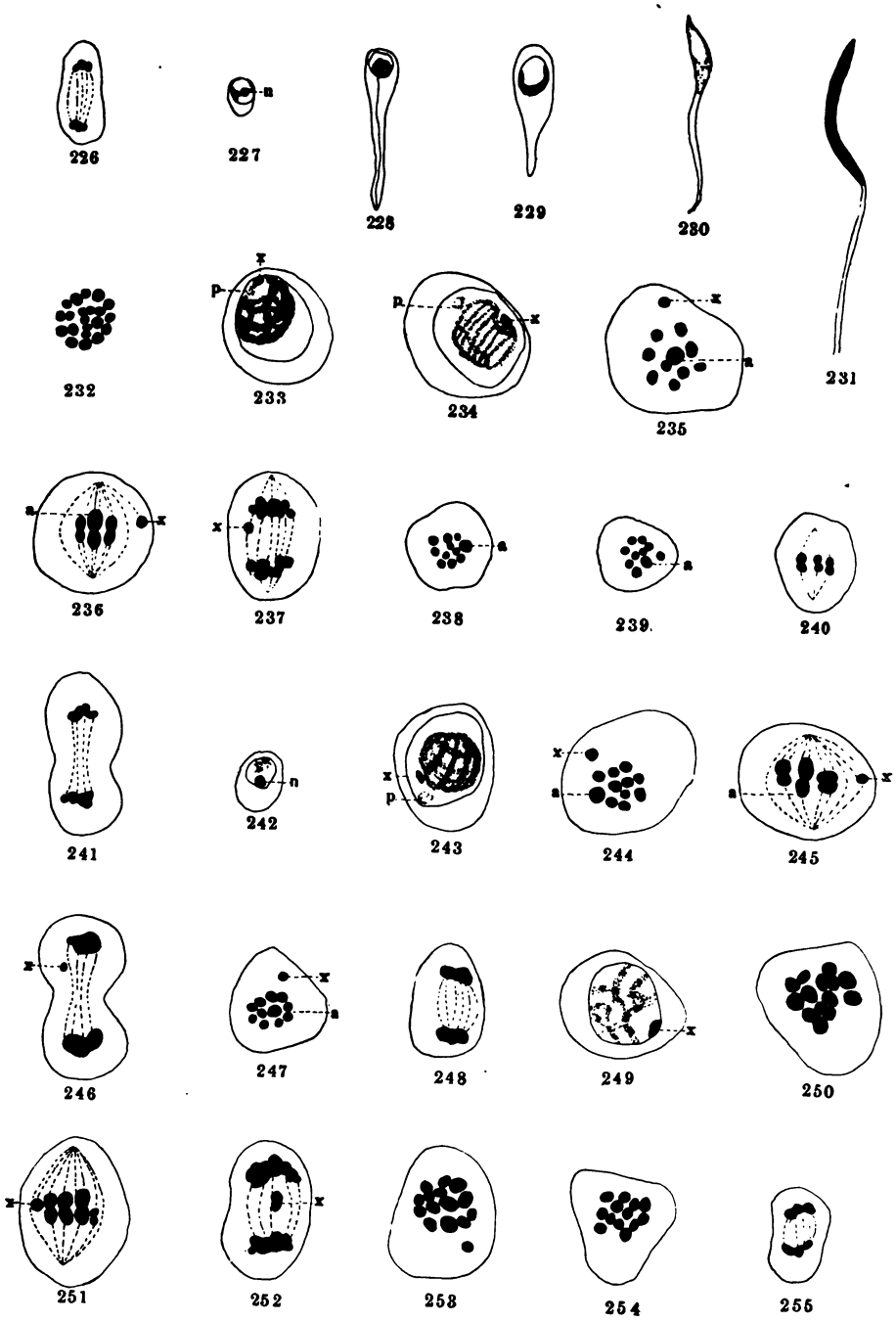
Fig. 250 First spermatocyte, equatorial plate, 14 chromosomes.

Fig. 251 First spermatocyte, metaphase.

Fig. 252 First spermatocyte, anaphase.

Figs. 253, 254 Second spermatocytes, equatorial plates, containing 14 and 13 chromosomes, respectively.

Fig. 255 Second spermatocyte, anaphase.



A. M. B. *del.*

CERCOPIDÆ

Plate VIII

Pœciloptera septentrionalis (*Family Fulgoridæ*)

Fig. 256 Spermatogonial rest stage.

Fig. 257 Spermatogonial split spireme.

Fig. 258 Spermatogonium, spireme segmented and condensed, segments split.

Fig. 259 Spermatogonial equatorial plate, 27 chromosomes.

Fig. 260 Spermatogonial metaphase.

Fig. 261 Spermatogonial anaphase.

Fig. 262 First spermatocyte, early synapsis stage.

Fig. 263 First spermatocyte, contraction stage.

Fig. 264 First spermatocyte, spireme stage.

Figs. 265, 267 First spermatocyte, rest stages, growth in size of nucleus and cell.

Fig. 268 First spermatocyte, split spireme stage.

Fig. 269 First spermatocyte, prophase, tetrad formation.

Fig. 270 First spermatocyte, equatorial plate, 14 chromosomes.

Fig. 271 First spermatocyte, metaphase.

Fig. 272 First spermatocyte, anaphase.

Figs. 273, 274 Second spermatocytes, equatorial plates, containing 14 and 13 chromosomes, respectively.

Fig. 275 Second spermatocyte, metaphase.

Fig. 276 Second spermatocyte, anaphase.

Figs. 277, 278 Spermatids, formation of fibers in the "Nebenkern."

Fig. 279a Spermatid, "Nebenkern" separated by a partition into two tubes.

Fig. 279b Cross section of "Nebenkern" structure as in 279a.

Fig. 280 Spermatid, elongation of fibers and tubes.

Fig. 281a Spermatid, irregular spiral of twisted tubes.

Fig. 281b Cross sections of tubes of 281a.

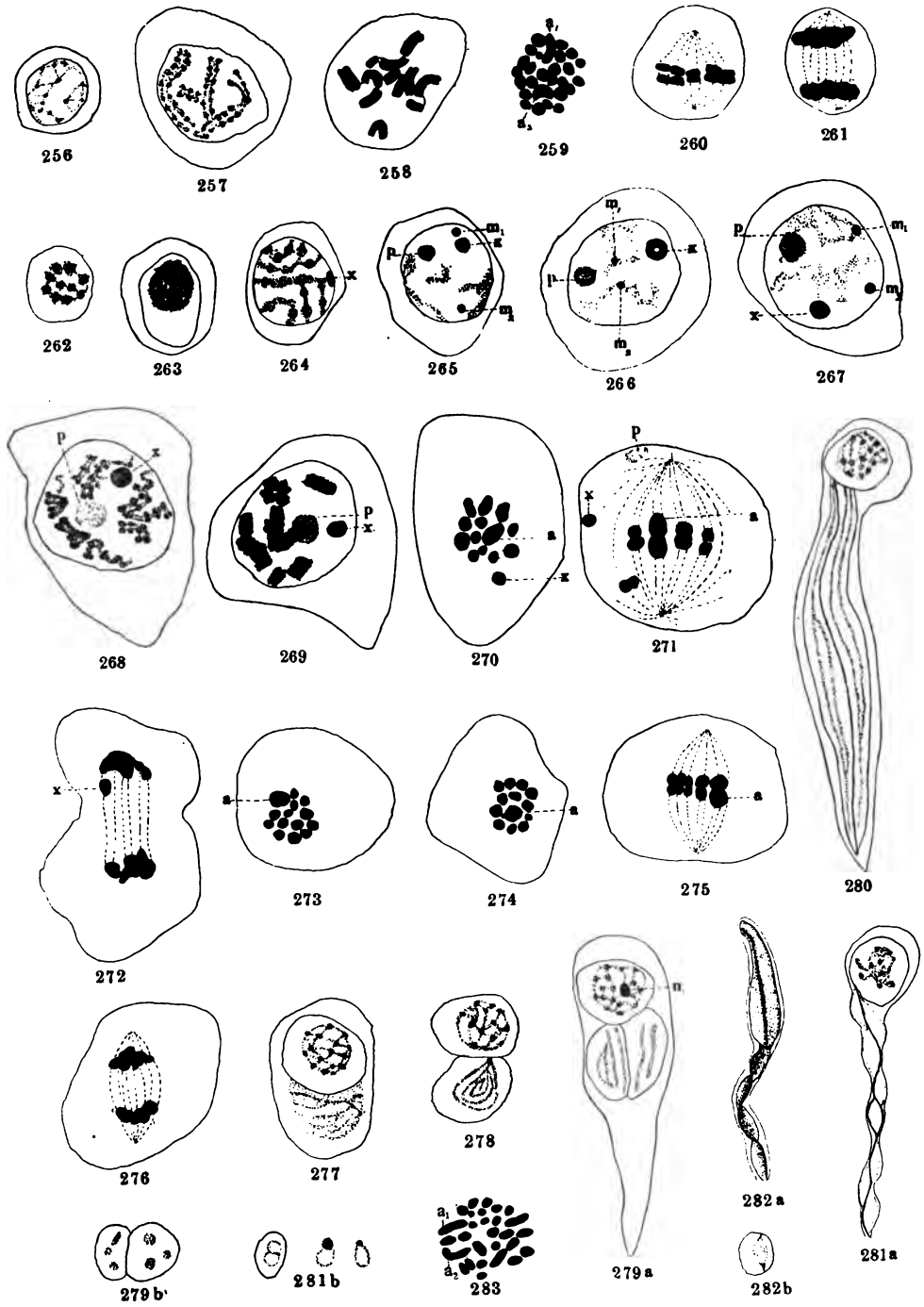
Fig. 282a Spermatid, further twisting and flattening.

Fig. 282b Cross section of 282a.

Fig. 283 Female somatic equatorial plate, 28 chromosomes.

SPERMATOGENESIS

ALICE M. BORING



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FULGORIDÆ

Plate IX

Pœciloptera pruinosa (*Family Fulgoridæ*)

Fig. 284 First spermatocyte, rest stage.

Fig. 285 First spermatocyte, equatorial plate, 14 chromosomes.

Fig. 286 First spermatocyte, metaphase.

Fig. 287 First spermatocyte, anaphase.

Figs. 288, 289 Second spermatocytes, equatorial plates, containing 14 and 13 chromosomes, respectively .

Fig. 290 Second spermatocyte, metaphase.

Fig. 291 Second spermatocyte, anaphase.

Figs. 292, 293 Spermatids, half with x, half without.

Fig. 294 Female somatic equatorial plate, 28 chromosomes.

Amphiscepa bivittata (*Family Fulgoridæ*)

Fig. 295 Spermatogonial equatorial plate, 25 chromosomes.

Fig. 296 First spermatocyte, rest stage.

Fig. 297 First spermatocyte, equatorial plate, 13 chromosomes.

Fig. 298 First spermatocyte, metaphase.

Fig. 299 First spermatocyte, anaphase.

Figs. 300, 301 Second spermatocytes, equatorial plates, containing 13 and 12 chromosomes, respectively.

Fig. 302 Second spermatocyte, metaphase.

Fig. 303 Second spermatocyte, anaphase.

Fig. 304 Spermatid.

Pœciloptera bivittata (*Family Fulgoridæ*)

Fig. 305 First spermatocyte, rest stage.

Fig. 306 First spermatocyte, equatorial plate, 13 chromosomes.

Fig. 307 First spermatocyte, metaphase.

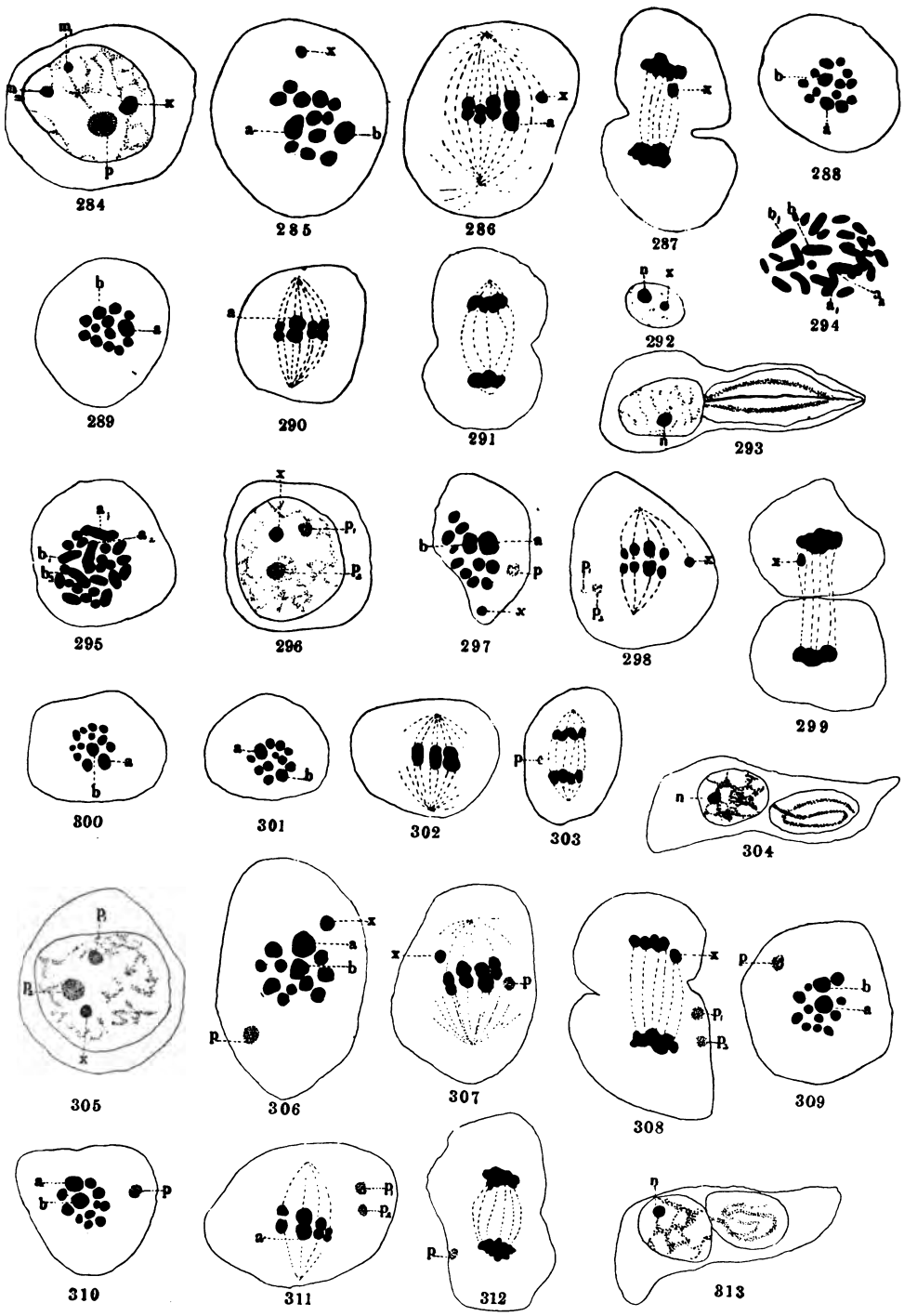
Fig. 308 First spermatocyte, anaphase.

Figs, 309, 310 Second spermatocytes, equatorial plates, containing 13 and 12 chromosomes, respectively.

Fig. 311 Second spermatocyte, metaphase.

Fig. 312 Second spermatocyte, anaphase.

Fig. 313 Spermatid.



A. M. B. *del.*

FULGORIDÆ